Symposia Biologica Hungarica 15

# LIMNOLOGY OF SHALLOW WATERS

Akadémiai Kiadó, Budapest

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15

# LIMNOLOGY OF SHALLOW WATERS

edited by

J. SALÁNKI and J. E. PONYI

(Symposia Biologica Hungarica 15)

According to estimations half of the population of the earth is undernourished for shortage of food in certain areas. Therefore, the International Biological Program (IBP) has set the aim of clarifying the basic processes of food production in the major ecosystems of the world.

At the same time, the increased exploitation of natural resources, and endeavours to promote the welfare of mankind are bound to endanger Nature's balance in this process. The fresh waters and fresh water life are also adversely influenced.

Being aware of these problems, the Biological Institute of the Hungarian Academy of Sciences at Tihany organized a Symposium on the Limnology of Shallow Waters in 1973. The organizers endeavoured to cover the whole range of shallow water production when they included in the program questions of bacterial production and breakdown, primary and secondary production, and the protection of water ecosystems. At the Symposium, the most outstanding research workers of two continents gave account of their latest results in 29 papers.

This volume will be of great use to those concerned with problems of production biology and water protection.

AKADÉMIAI KIADÓ
Publishing House of the Hungarian Academy of Sciences, Budapest

ISBN 963 05 0427 8

Symposia
Biologica
Hungarica
15

# Symposia Biologica Hungarica

Redigit

J. SALÁNKI et J. E. PONYI

Vol. 15

AKADÉMIAI KIADÓ, BUDAPEST 1975

# LIMNOLOGY OF SHALLOW WATERS

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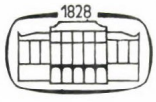


AKADÉMIAI KIADÓ, BUDAPEST 1975

Proceedings of a Symposium held at the
Biological Research Institute of the
Hungarian Academy of Sciences in Tihany,
3rd–8th September, 1973

ISBN 963 05 0427 8



Printed in Hungary

# FOREWORD

The papers delivered at the Symposium of Limnology of Shallow Waters held between 3rd–8th, September 1973 at the Biological Research Institute of the Hungarian Academy of Sciences, in Tihany at Lake Balaton deal with problems interesting not only for hydrobiologists but also for other biologists engaged in the field of environmental research. The International Biological Programme stimulated directly or indirectly certain of the contributions presented here, drawing attention, particularly, to the problems of freshwater ecosystems. A further programme supported by international authorities, called Man and Biosphere (MAB) strongly hopes for the continuation of these investigations. Our joint aim in publishing this material is to make available the results discussed at our meeting to a wider scientific community, in the earnest desire that it will contribute to better information concerning latest results as well as to the stimulation of further research on the present life of standing waters endangered by the many harmful factors of our age.

The Hungarian Academy of Sciences deserves special gratitude for the financial support of the Symposium. We also wish to express many thanks to all contributors and to our colleagues for their help in organizing the Symposium and for their technical assistance in preparing this volume, especially to Drs P. Biró, S. Herodek, J. Oláh, Nóra P.-Zánkai and Mrs. Judith Komáromi.

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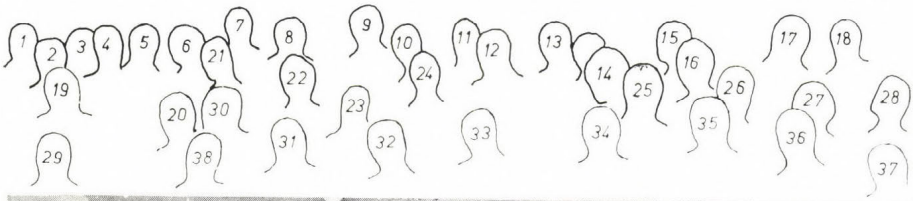
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# OPENING ADDRESS

by

J. Salánki

DIRECTOR OF THE BIOLOGICAL RESEARCH INSTITUTE OF THE HUNGARIAN ACADEMY OF SCIENCES, TIHANY, HUNGARY

Ladies and Gentlemen, dear Colleagues,

It is a great pleasure for me to welcome the participants of the Symposium on Limnology of Shallow Waters, here at the Biological Research Institute of the Hungarian Academy of Sciences.

As you probably know, one of the reasons for founding this Institute at the shore of Lake Balaton—the largest lake in Central Europe—was to enable intensive investigations on the biology of the lake to be carried out. Over the past 46 years extensive research has been done at the Department of Hydrobiology, and up to now some five hundred papers have been published on the flora and fauna of the Balaton and also on various problems concerned with its systematics, ecology, production and pollution. These papers have mainly appeared in the annual journal 'Annales Instituti Biologici (Tihany)'.

As a result of a growing interest in environmental biology throughout the world during the past several years our work on hydrobiology has also been intensified. We feel that in addition to extensive investigations, the development of international cooperation and mutual discussions in this field are also of paramount importance for more profitable research. It is for this reason that our Institute decided to organize this meeting and we are very glad that you accepted our invitation both to attend and to present papers.

In the hope that this Symposium will be successful both from the scientific viewpoint and in promoting further personal contact between the participants, from many parts of the world, I welcome you once again, wishing you interesting and absorbing lectures, fruitful discussions and pleasant, sunny days at this beautiful part of Hungary.

*Symp. Biol. Hung.*, *15*, p. 17 (1975)

# WELCOMING ADDRESS

by

B. Zólyomi

MEMBER OF THE HUNGARIAN ACADEMY OF SCIENCES, DIRECTOR OF THE INSTITUTE OF BOTANY OF THE HUNGARIAN ACADEMY OF SCIENCES, VÁCRÁTÓT, HUNGARY

Ladies and Gentlemen,

It is an extremely great honour for me to welcome you on behalf of the Biological Section of the Hungarian Academy of Sciences.

On the occasion of this Symposium let me make some preliminary remarks.

The problems of human environment (natural and artificial) are universally of current interest. It is for this reason that a scientific approach to these problems is of extreme importance.

It is worth mentioning that, e.g. the MAB (Man and Biosphere) programme, i.e. the scientific programme of UNESCO, is at the same time global and regional, at the governmental and non-governmental levels. Programme 5 on the 'Ecologic effect of human activities on the values and resources of lakes, moors, rivers, deltas, estuaries and costal zones' may also be of interest. The Hungarian Academy of Sciences has established, a.o. a research project on the 'Protection of man and his natural environment'. This plan having been adapted to the MAB programme is simultaneously concerned with terrestrial and aquatic ecosystems.

A highly alarming deterioration of the environment results from pollution in general, particularly from the contamination of rivers and lakes. Shallow waters are most strongly affected by this process. This is the reason why, in my opinion, this Symposium is of special importance.

On behalf of the Hungarian Academy of Sciences I wish you fruitful work.

# I. PRIMARY PRODUCTION

*Symp. Biol. Hung.*, *15*. pp. 21–27 (1975)

# RELEASE OF PLANT NUTRIENTS FROM REED BORDERS AND THEIR TRANSPORT INTO THE OPEN WATERS OF THE BODENSEE-UNTERSEE

by

R. Schröder

LANDESSTELLE FÜR GEWÄSSERKUNDE UND WASSERWIRTSCHAFTLICHE PLANUNG, INSEL REICHENAU, FRG

Lake Constance, the second largest lake in the region of the Alps, has a surface area of 540 km$^2$ and a maximum depth of 252 m. It measures about 69 by 15 km, its total water volume being 49.3 km$^3$.

The lake is divided into two parts which are connected by the Seerhein at the city of Constance. The smaller part, the Untersee, is only 66 km$^2$ large, its maximum depth is 46 m, while the average depth covers 28 m. The Untersee is an originally eutrophic lake with broad littoral zones and a circumference being 3.2 times greater than a circular area of equal extension; there are two peninsulae and one island.

Lake Constance receives its water mostly from the Alps where it is partly bound as snow and ice during winter-time to be released in spring and summer. In the same period the greatest precipitation also occurs in a watershed of nearly 11,000 km$^2$ (6,560 km$^2$ belonging to the Rhein). This is the reason why the lake level varies with a mean amplitude of about 1.5 m. From time to time, extremely high water levels occur which cause devastation to agriculture and villages. To cut the peaks of extremely high water levels and to provide the ship-traffic on the outflowing Rhein with a more or less equal quantity of water, a project is being formulated to regulate the outflow. This means a change of the flow rate in the lake and an alteration of the seasonal altitude of the level of the Untersee. The proposed annual line of the lake level would be some centimetres higher than at present with an additional change in the form of the lake. The spring rise would arrive earlier with a higher level in autumn. In general, more land would be flooded. As the shores of the Untersee are rather flat, one centimetre in the altitude of the lake level corresponds to 12.45 ha, which is 0.7 per cent of the area within the annual tidal range.

These reflections initiated the investigation of the eutrophying part of the littoral zone, though it was clear that its effect could be only of minor importance compared with the eutrophying inflow from sources of civilization.

How high is the rate of plant nutrient release from the zones being situated in the range of the possibly regulated lake level? These areas in the Untersee are mostly covered with reed (*Phragmites communis*). Among the plants plastic cylinders were exposed which enclosed one-third m$^2$ of the lake bottom and 100 to 200 litre of lake water. They were closed on top. Temperature and oxygen were measured and daily water samples were taken at 9 a.m. The samples were immediately examined.

The concentrations of dissolved phosphorus in the surroundings of the

cylinders were between 5 and 79 $\mu$g per litre for total P, and 2 and 70 $\mu$g per litre for $PO_4$-P. They were the 'blanks' for the experiments in which daily changes were measured. The daily changes varied synchronously in the three cylinders so that they could be caused by external influences only. The cylinders being translucent, a part of the released P could immediately be consumed by assimilation. This is confirmed by the concentration of the dissolved oxygen, which followed the same trend. The metabolism in the cylinder depending on light intensity, phytoplankton concentration and bacterial activities is highly complicated and needs special investigations. We examined the output of the 'black box', which is the amount of released material minus the part immediately incorporated into biomass within 24 hours. This is also the daily rate actually passing into the lake water. From all experiments the average rate of released phosphorus is 4.4 mg per $m^2 \cdot$ day, 90 per cent of which appears in the form of $PO_4$-P (Table 1).

TABLE 1

*Daily rate of released phosphorus and mineral nitrogen in 11 experiments*

| | 8th–11th June | 13th–18th June | 27th–29th June | 29th June–5th July | 8th–12th July | 12th–16th July |
|---|---|---|---|---|---|---|
| Total P | −1.01 | +1.24 | +7.57 | +0.52 | +5.95 | +15.05 |
| $PO_4$-P | −0.46 | +0.06 | +4.84 | +0.14 | +6.11 | +13.47 mg/m² · d |
| N min. | +47.34 | +11.58 | +6.38 | −23.42 | +21.02 | +17.08 |
| | 16th–19th July | 26th–30th July | 30th July–3rd August | 3rd–7th August | 7th–13th August | average 8th June–13th August |
| Total P | +9.48 | +0.91 | +5.14 | +2.62 | +1.94 | +4.4 |
| $PO_4$-P | +7.35 | +1.07 | +5.28 | +3.48 | +1.87 | +4.0 mg/m² · d |
| N min. | +14.02 | +4.54 | +52.66 | −3.00 | +1.03 | +8.05 |

In the experiment lasting from 8th to 11th June, the amount of P decreased, i.e. assimilation bound more P than had been released by the bottom during the same period. After the experiment it was observed that the cylinder was exposed on a stony ground being covered only with a thin layer of organic material.

In four experiments (8th–12th and 26th–30th July, 30th July–3rd August and 3rd–7th August), the daily increase of $PO_4$-P was greater than that of total P. Either the last stage of P-mineralization ran faster than the previous stages, or the $PO_4$-uptake by primary producers was less in this time than in the other experiments. There was no correlation with the light conditions. Therefore, it can be assumed that this is due to the density of the phytoplankton population as confirmed by the measurements of its chlorophyll content.

The total concentration of mineral nitrogen-compounds ($NH_4$ + $NO_2$ + + $NO_3$-N) in general increases during the experiments, on the average by 8.05 mg per $m^2 \cdot$ day. As oxygen concentration generally decreases,

the relationship between $NO_3$-N and $NH_4$-N shifts towards ammonia. Therefore, the experiment was stopped when oxygen concentration reached approx. 1 mg per litre, a minimum value under natural conditions in the reeds. Figure 1 demonstrates two experiments under different weather conditions. In the first case, oxygen and nitrate concentrations decreased with ammonia increasing. The total concentration of N increased from 931 to 1,607 $\mu$g per litre in three days. The weather was bad with an overcast sky. In the second case, the oxygen concentration did not fall very much, with a rise toward the end of the complete experiment. The ammonia curve returned to the initial point after small variations. The nitrate concentration rose from

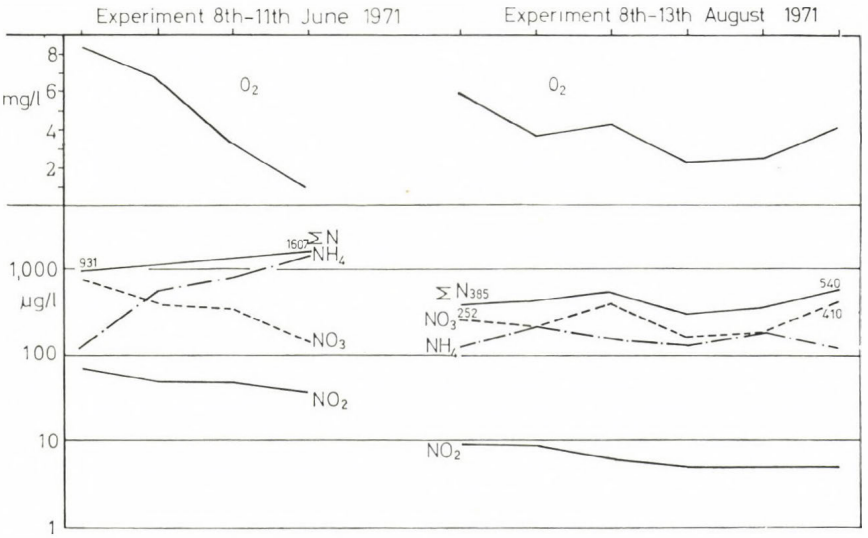


Fig. 1. Experiments with decreasing and varying oxygen concentration

252 to 410 $\mu$g per litre. The released nitrogen consisted primarily of nitrate-compounds. The total amount of these N-compounds increased from 385 to 540 $\mu$g per litre in five days. This experiment was made in favourable weather conditions. In these processes also the composition of the soil, bacteriological conditions and the kind of water might play an important role.

Where do the released substances come from? In the reed area several sediment cores were taken and the interstitial water was analysed. A concentration of dissolved total phosphorus ranging from 20 to 410 $\mu$g per litre (mean 130 $\mu$g per litre) was found, about 50 per cent of which was $PO_4$-P. In general, the concentration in the upper layer of the core is 2–3 times higher than in the deeper layers. Above all, the organic P-compounds decrease with depth.

Nitrate and ammonia also become less concentrated in deeper layers. Both compounds run parallel, but there is nearly four times more ammonia than nitrate. The concentrations of ammonia varied between 720 and 8,000 $\mu$g per litre (mean: about 2,500 $\mu$g per litre) and those of nitrate between 160 and 2,800 $\mu$g per litre (mean: 660 $\mu$g per litre).

The content of interstitial water was about 80 per cent on top of the core, although in layers deeper than 10 cm it varied between 25 and 35 per cent. The amount of organic matter was around 4 per cent on top, and in the depths (at more than 10 cm) it was 0.6 to 1.0 per cent.

The mineral part consists of marl, containing 0.01 to 0.05 per cent phosphorus in several forms. The rhizomes of *Phragmites* can reach a depth down to 1 m. This means that under 1 $m^2$ the stock of bound phosphorus is approx. 160 to 800 g (if the sediment contains 30 per cent of water and has a specific weight of 2.25). According to the equilibrium of aqueous solutions, P is exchanged between the sediments and the interstitial water so that the consumed P of the interstitial water can easily be replaced. This is necessary because the dissolved P is only 40 mg per $m^2$ up to a depth of 1 m, being not enough to completely satisfy the plant requirements. From these calculations it can be assumed that external factors (such as agricultural fertilizers, sewage, etc.) can be excluded. This is not surprising, as many reed swamps grow far away from external nutrient supply.

The total phosphorus in the interstitial water contains about 50 per cent $PO_4$-P, the total P released from the bottom containing, however, 90 per cent. Beside that, the daily release is so high that it is improbable that the total amount of P released comes directly from the interstitial water of the soil. A great part must be released by a decaying organic matter covering the bottom of the reeds, mostly by dead *Phragmites*-stalks. Therefore, the route of P from the ground to the lake water seems to be as follows (Fig. 2). Bound to minerals, interstitial water, rhizomes, plants, in which it is fixed for one year till the stalk dies, falls into the water and decays, and is then released into the lake water in the reeds.

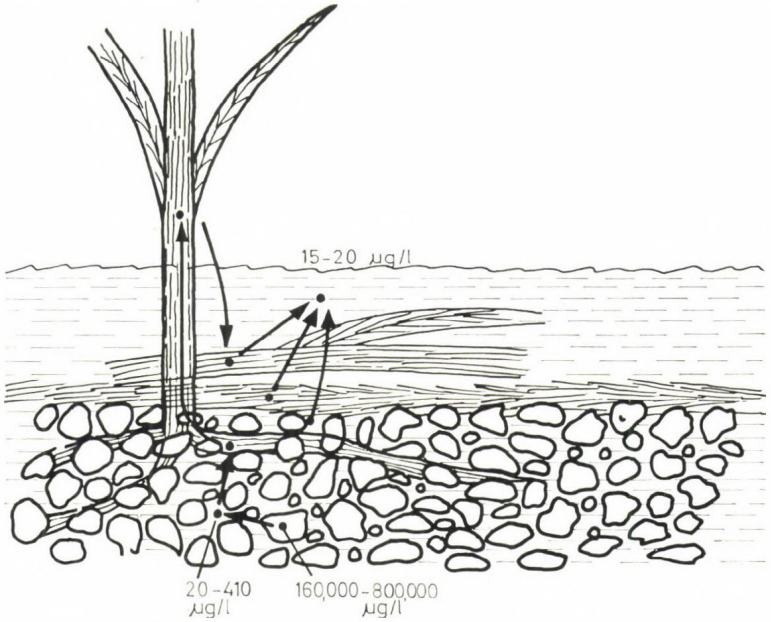


Fig. 2. Route of phosphorus from the mineral stage into the water of the reeds

What happens to the nutrients in the lake water in the reed area? In three sections across the reed swamp the surface and bottom water were stained with a fluorescent dye to measure its speed and to determine its direction. It could be demonstrated that there were two currents running perpendicular to the shore line: A surface current, coming from the lake and a bottom current directed towards the lake (Fig. 3). These currents

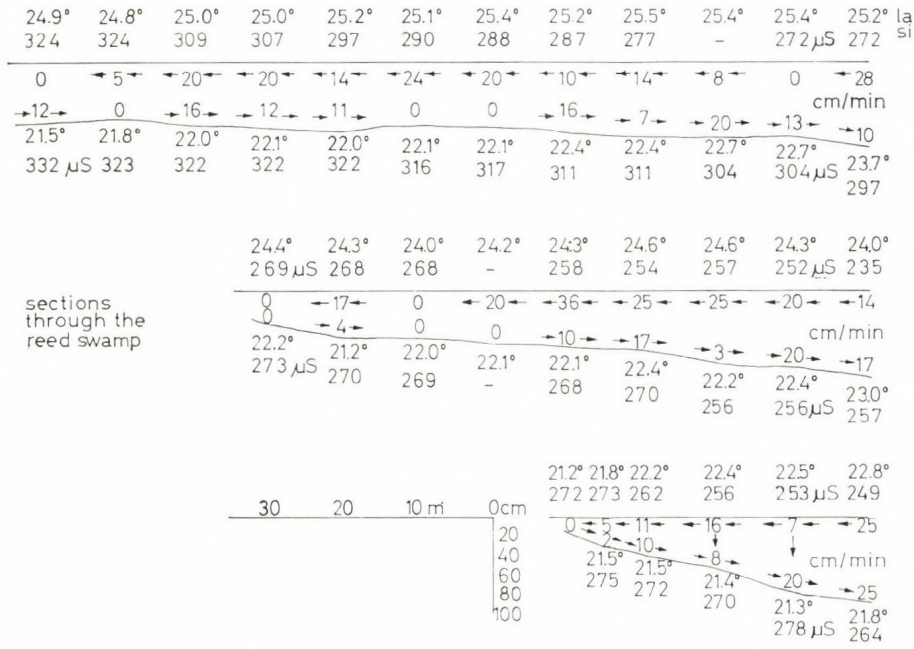


Fig. 3. Temperature, conductivity and speed of currents

can always be observed in warm weather. Their velocities vary from 0 to 36 cm per min at the surface, and to 25 cm per min near the bottom. Cold and cloudy weather can markedly reduce the speeds, extremely high warming during sunny summer days can induce speeds up to 150 cm per min.

The temperatures along the sections diminish from the open lake to the shore and show a difference between the surface and bottom currents. There is also a difference in the conductivity between both currents of up to 30 $\mu$S.

It is presumed that the driving force for their movement is the increased density of water due to the shading effect of plants, specifically their cooling effect, and to the enrichment of dissolved material. The weak inclination of the bottom seems to be sufficient to let the heavier bottom water glide lakewards. The lighter lake water is drawn into the reeds.

The water exchange on the shelf outside the reeds has been known since Pichler (1938) and Thomas (1961), but there, the water moves the other way round (Fig. 4). Warm surface water from the shelf is directed towards the lake being replaced by cold bottom water. This must be due to warming,

because at night the currents reverse their direction. Substances released into the water of the reeds, in any case, are carried into the open lake.

How much nutrient is brought from the littoral to the pelagic zone of the lake? As already mentioned, the extension of the littoral zone depends directly on the lake level. The annual mean area measures about 14 km² and the pelagic part with a depth of more than 1 m is 52 km², being 3.7

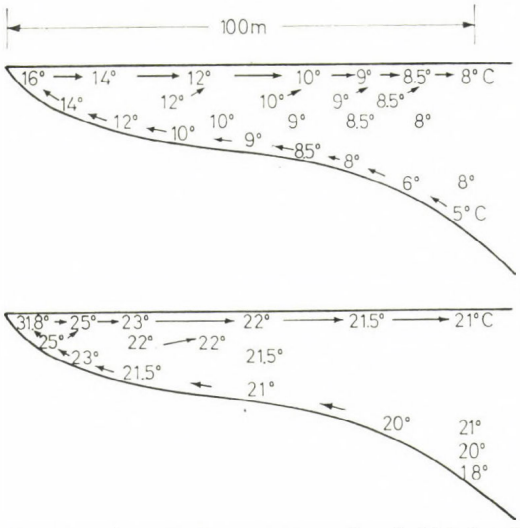


Fig. 4. Temperatures and way of currents on the shelf (after Thomas 1961)

times that of the littoral area. More than one-third of the shallow part is covered with reed. The other parts are occupied by more or less dense populations of Potamogeton species and *Najas marina* during summer.

Assuming that the daily rate of nutrient release over the whole littoral zone is 4.4 mg per m² total P and 8 mg per m² mineral N, one m² of lake area receives yearly 340 mg dissolved P and 620 mg N. Since the mean depth of the Untersee is 28 m, the amount of P from the littoral zone would be enough to give the lake a mesotrophic stage, according to Vollenweider's correlation. The individual basins of the lake being more or less isolated by peninsulae, an island and shallow barriers would have trophic levels ranging from 'still oligotrophic' to 'eutrophic' in different parts. This is exactly what was found in 1935.

Today the lake area receives about 3 g P per m² and per year from waste waters, which is nearly 10 times that introduced by natural nutrient sources. Thus, they do not seem to be of much importance. By the annual fluctuations of the lake level, however, the flooded area and therefore the monthly input of nutrients in the lake change (Fig. 5), with a minimum in the winter months and a maximum in summer. On the other hand, the P concentration in the open lake shows a reverse trend, so that a low concentration in the lake meets with a high output from the littoral zone. The coincidence of these two systems does not affect the total P budget of the lake but can lead to local eutrophying effects along the shore line. In summertime the

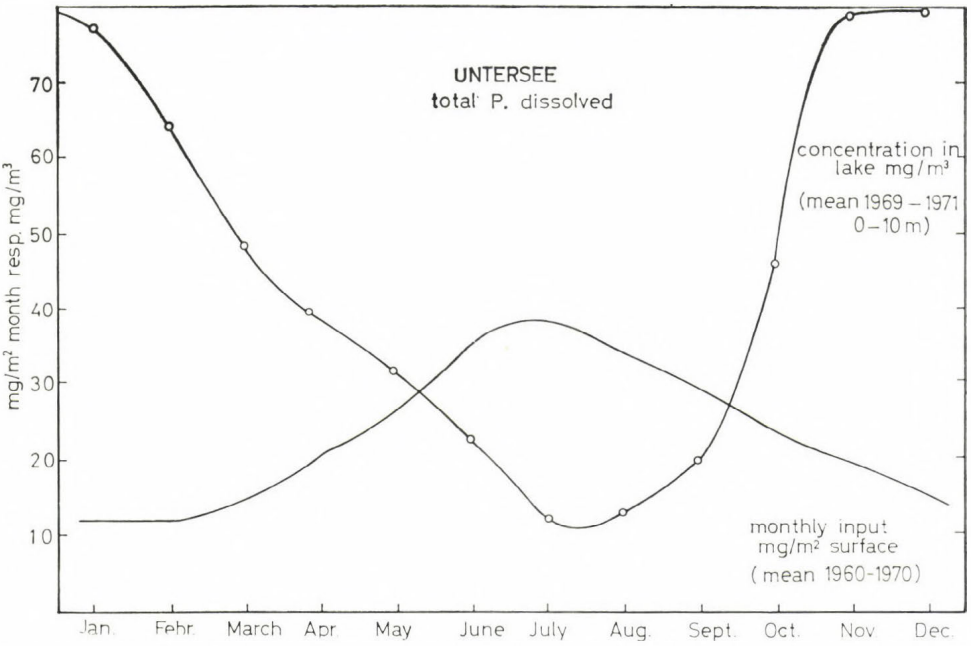


**Fig. 5. Monthly input and concentration of dissolved phosphate in Lake Untersee**

P concentrations in the proximity of the reed swamp are actually 2 to 3 times higher (45 $\mu$g per litre) than in the pelagic area (18 $\mu$g per litre). This, together with high water temperatures, causes a strong development of filamentous algae nourished by the bottom current. They provide the visual evidence of the effect of the reed borders.

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*Symp. Biol. Hung.*, *15*, pp. 29–34 (1975)

# PHYTOPLANKTON PRODUCTION IN LAKE BALATON

by

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Several papers (Entz et al. 1937, Sebestyén et al. 1951, Sebestyén 1953, 1954, Tamás 1955, 1967, 1969) deal with the quantity of planktonic algae of Lake Balaton. Nevertheless, only preliminary data collected in 1961 (Böszörményi et al. 1962) have been available on the primary production of the lake.

In April 1972, we started to study the annual cycle of phytoplankton production in the pelagic zone of the lake, two kilometres eastwards of Tihany. Investigations were carried out fortnightly, irrespective of the weather. Water samples were taken in 250 ml glass flasks at depths of 25, 100, 200 and 300 cm. Of this water 100 ml was transferred into pyrex glass flasks for exposal. The remaining water was conserved by $J_2$/KJ and served algological determinations.

Algae were counted by Utermöhl's plankton microscope. The biomass of each species was determined by Lohmann's volumetric method, i.e. the volumes of the average individuals were determined and these values were multiplied by the number of individuals in the sample.

To each sample used in primary production measurement 20 $\mu$Ci $Na_2{}^{14}CO_3$ (specific activity 290 $\mu$Ci per mg) was added. The samples were lowered to their original places, and exposed *in situ* for four midday hours. Dark parallels were also prepared. After four hours' exposal the samples were placed in a dark box, transferred to the laboratory and filtered through a membrane filter of a pore size of 0.2 $\mu$ (Sartorius Membranfilter GmbH).

In order to remove radioactive contamination subsequently to the samples 50 ml of previously filtered inactive lake water was passed through the filters being exposed to the fumes of concentrated HCl for four minutes. The filters were then dissolved in 10 ml Bray solution, the algae forming a fine suspension in this liquid. Radioactivity was measured by liquid scintillation which has several advantages over the GM tube technique. The weight of the carbon taken up by the phytoplankton was calculated from the radioactivity of the algae and from the specific activity of the total carbonic acid content of the water, allowing a 5 per cent isotope effect. Each value was reduced by that of the dark parallel.

In the water samples collected during the 25 experimental days from the four different depths, altogether 124 algal species, 6 varieties and 1 form were found. Their distribution among the phyla was as follows: Cyanophyta 13, Euglenophyta 11, Pyrrophyta 6, Chrysophyta 61, Chlorophyta 40. The biomass of the most important species is given in Fig. 1. The plankton is generally dominated by diatoms. One single species,

*Cyclotella bodanica*, amounted to half of the total biomass for a long period. Toward the middle of summer it was replaced by *Melosira granulata*. Among the Pyrrophyta algae, *Ceratium hirundinella* is the most important species, dominating the summer plankton in this lake. Concerning their biomass Euglenophyta, Chlorophyta and Cyanophyta phyla are inferior. Benthic elements are usually found but in limited number in the plankton.

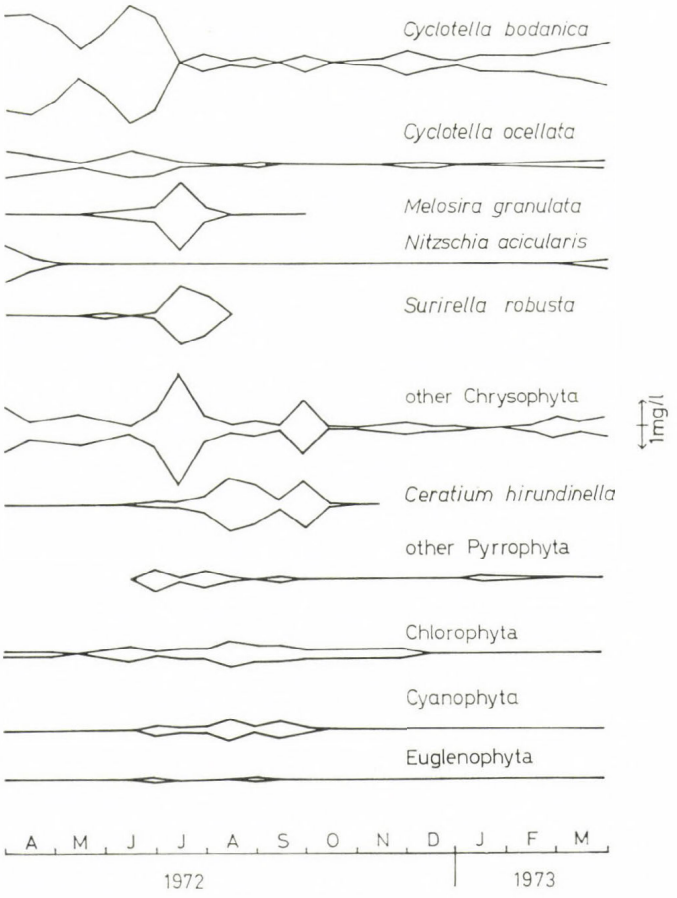


Fig. 1. Biomass of the dominant algae

However, the heavy storm on 11th July swirled up huge quantities of algae from the bottom, doubling the biomass of phytoplankton. That day, the largest mass was represented by *Surirella robusta*.

The annual cycle of the total biomass of phytoplankton (Fig. 2) showed two maxima, one in April and the other in June–July. The summer biomass attained 4 mg per litre. This value is one order of magnitude higher than that in the forties (Tamás 1955) indicating the rapid process of cultural eutrophication. In autumn the biomass showed a rapid decrease remaining around 0.5 mg per litre in autumn and winter. In January and in the first decade of

February the lake was frozen. After the thawing of the ice the amount of algae increased again. In Fig. 2 the columns are divided according to the mass of algae belonging to the groups of different size. Their production has not been separately studied yet. The largest fraction of the total biomass is constituted by species which, owing to their size, are not available as food to the crustacean plankton.

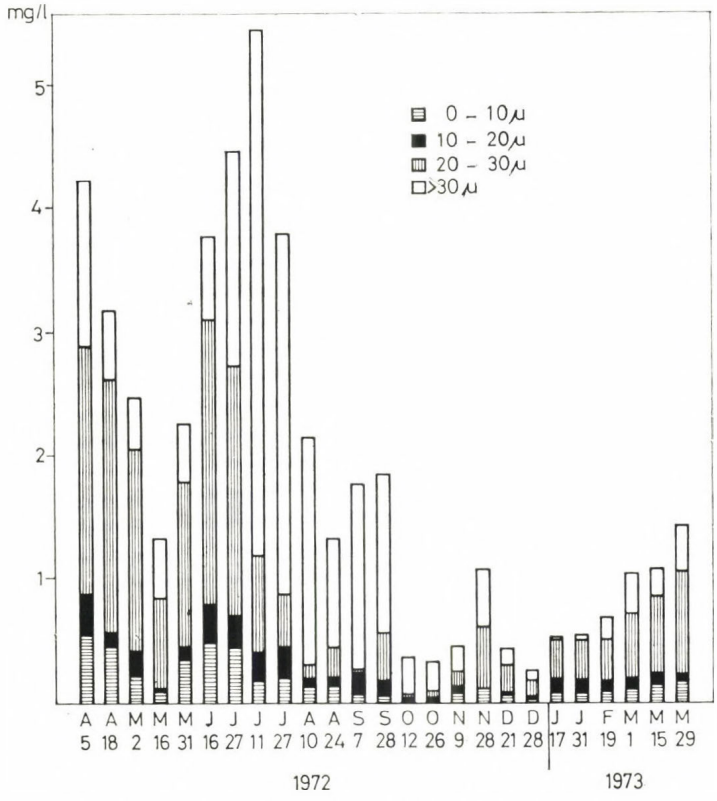


Fig. 2. Annual cycle of the biomass of phytoplankton

The vertical distribution of the phytomass was always uneven, but in the average values of the 25 days there were no differences as to the depth.

The vertical distribution of the primary production (Fig. 3) showed the most diverse figures. The maximum was sometimes at 25 cm, sometimes at 1 or 2 m, or in the deepest sample even at 3 m. This peculiarity is explained by the shallowness of the lake. Very strong waves can rise on the 600 km$^2$ surface of the lake. On the other hand, the water is only 3–4 m deep, therefore the waves turn the whole lake upside down bringing a lot of mud into the water. The transparency of the water is a function of the amount of suspended mud being usually low, and highly variable (Table 1), the illuminance of the deeper layers depending more upon waves than upon clouds. In the storm only 2 per cent of light penetrated into the 1 m depth,

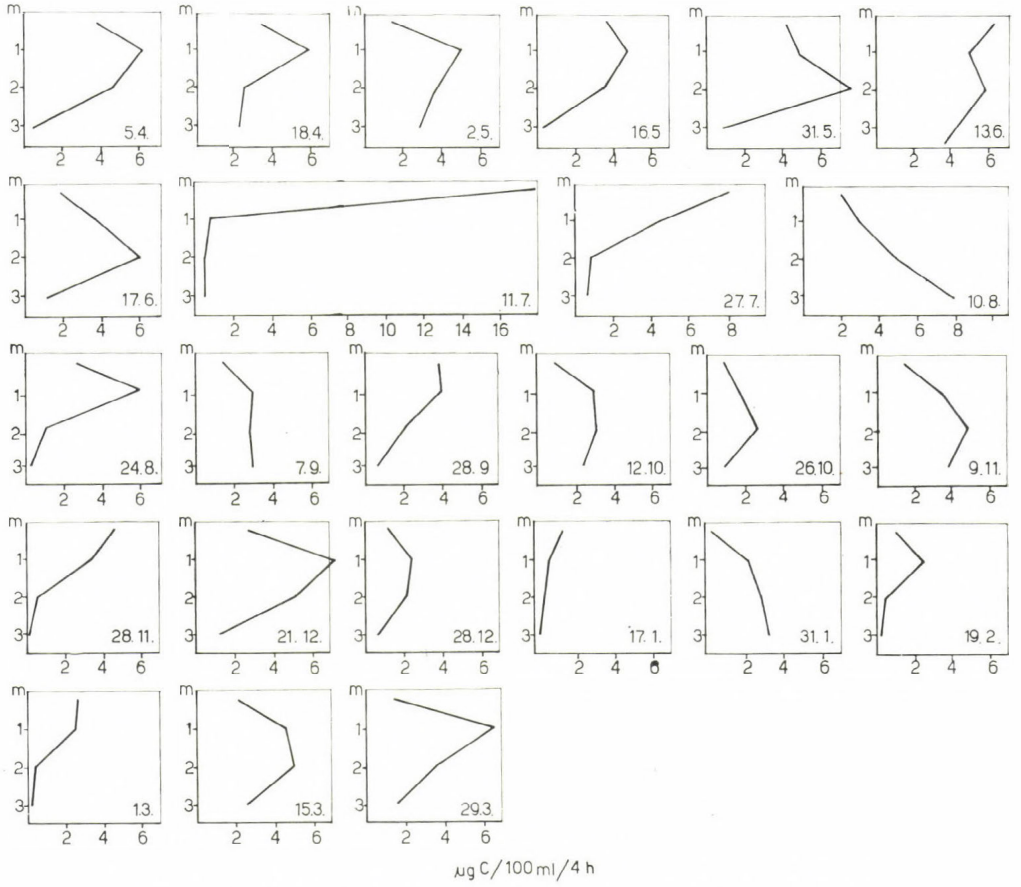


Fig. 3. Vertical distribution of the planktonic primary production

while after a long calm, 20 per cent of surface illuminance was measured at the bottom. Most frequently there is photoinhibition at the surface, the maximal production being at 1 or 2 m, and in two-thirds of all cases there is little if any production at a depth of 3 m.

From the values obtained at the four depths the production per surface area was calculated and extrapolated for the day-time hours (Fig. 4). From April to August the production was uniformly high. In this period the maxima and minima reflect not so much the real seasonal changes as the actual weather conditions of the experimental days. In calm, when the whole water column is light saturated, the production per surface area is high, while in storm the euphotic layer being restricted to the upper 1–2 m, the production is low. From the middle of August the production decreased and remained low in autumn and winter. Maxima were found on calm days in this period, too. The absolute minimum of production was found under the snow-covered ice. Under snow-free ice the planktonic production was quite considerable and at the optimally illuminated bottom

TABLE 1

*Illumination in different depths in percentage of surface illumination*

| Dates \ Depths (cm) | 25 | 100 | 200 | 300 | bottom |
|---|---|---|---|---|---|
| 5th Apr. | — | — | — | — | — |
| 18th Apr. | 50.0 | 23.4 | 3.9 | 0.8 | — |
| 2nd May | 64.7 | 26.5 | 7.3 | 1.0 | — |
| 16th May | 59.5 | 29.8 | 8.3 | 2.6 | — |
| 31st May | 63.1 | 14.8 | 4.2 | 1.6 | 0.9 |
| 13th June | 55.6 | 30.6 | 13.9 | 5.5 | 2.8 |
| 27th June | 53.0 | 26.5 | 6.3 | 1.8 | 0.9 |
| 11th July | 40.0 | 2.0 | 0.0 | 0.0 | 0.0 |
| 27th July | 59.0 | 6.9 | 1.1 | 0.1 | 0.0 |
| 10th Aug. | 82.1 | 48.2 | 32.1 | 19.6 | 12.1 |
| 24th Aug. | 61.4 | 6.8 | 1.4 | 0.3 | 0.1 |
| 7th Sept. | 70.8 | 43.8 | 24.0 | 12.5 | 8.3 |
| 28th Sept. | 57.5 | 12.5 | 2.5 | 0.5 | 0.3 |
| 12th Oct. | 67.5 | 30.0 | 15.0 | 7.5 | 6.0 |
| 26th Oct. | 73.8 | 28.3 | 15.2 | 7.4 | 6.5 |
| 9th Nov. | 79.6 | 40.7 | 22.2 | 11.1 | 9.3 |
| 28th Nov. | — | — | — | — | — |
| 21st Dec. | 64.6 | 15.6 | 2.1 | 0.3 | 0.1 |
| 28th Dec. | 70.0 | 13.7 | 3.1 | 0.8 | 0.4 |
| 17th Jan. | 9.2 | 3.3 | 1.5 | 1.0 | 0.8 |
| 31st Jan. | 42.9 | 30.0 | 20.7 | 12.9 | 8.6 |
| 19th Febr. | 42.5 | 5.4 | 0.5 | 0.0 | 0.0 |
| 1st March | 52.6 | 6.3 | 0.6 | 0.0 | 0.0 |
| 15th March | 69.4 | 34.0 | 12.5 | 3.5 | 2.1 |
| 29th March | 58.4 | 16.7 | 6.3 | 2.1 | 1.2 |

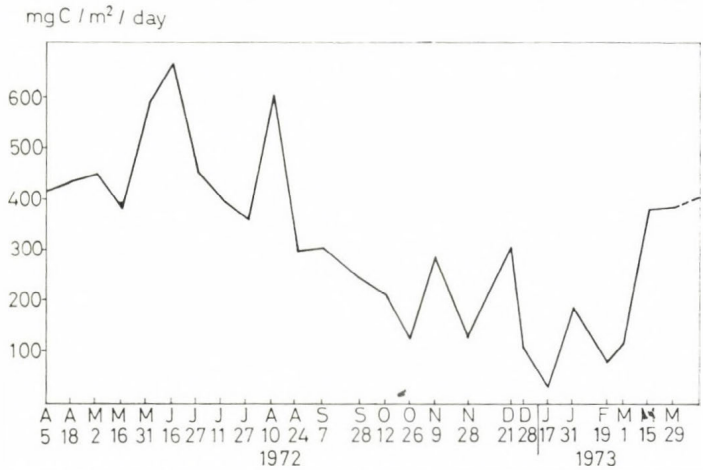


Fig. 4. Annual cycle of phytoplankton production

an even higher benthic primary production was observed (Herodek and Oláh 1973). In the unfrozen lake there is usually no measurable benthic photosynthesis due to turbidity. There was no sudden increase in the planktonic primary production when the ice thawed, but in the second half

of March it reached the high level of the previous spring. The highest production measured in these investigations was 669 mgC per $m^2$ per day. In the warmer half-year the mean daily production was 432 mgC per $m^2$. The annual production was 114 gC per $m^2$. This annual primary production corresponds to that of the moderately eutrophic lakes (Vinberg 1961, Rodhe 1969). The production in most parts of the lake is probably similar to that of this investigated area.

The most eutrophicated part of Lake Balaton is the Bay of Keszthely where the River Zala enters the lake. Here we started to study the primary production in June, 1973. In this part of the lake the maximal production was always at 25 cm, at 1 m the production was only half of that and, at 2 m and below it, there was practically no production due to the shading effect of algae. The production showed a high peak in July reaching 15 gC per $m^2$ per day. The total production in the three summer months was 700 gC per $m^2$. The productivity of this area seems to be one order of magnitude higher than it was twelve years ago, corresponding to that of the highly polluted eutrophic lakes. The process of cultural eutrophication calls for urgent counter-measures.

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*Symp. Biol. Hung.*, *15*, pp. 35–48 (1975)

# THE RELATIONSHIP OF PRIMARY PRODUCTION TO BASIN MORPHOMETRY IN FIVE SMALL OLIGOTROPHIC LAKES IN TERRA NOVA NATIONAL PARK IN NEWFOUNDLAND

by

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## INTRODUCTION

Rawson (1939) suggested that edaphic factors determine the primary trophic state of a body of water while basin morphometry, particularly mean depth, and the climate to a considerable extent, determine the utilization of the 'nutritive materials'. Deevey (1940) also stressed the importance of recognizing primary and secondary trophic states.

Ohle (1956), when discussing bioactivity, production and energy utilization in lakes, showed that the efficiency of energy utilization in a lake is directly proportional to its mean depth, or, the amount of potential energy eliminated from a lake by sedimentation as a percentage of the total potential energy available is inversely proportional to its mean depth. He concluded that the quantity of organic carbon deposited per unit time, per unit surface of basin is proportional to the quantity of organic carbon that is present during the same time interval per unit volume of the total lake. The larger the volume in relation to the mean depth of the basin, the smaller will be the percentage of autochthonous organic matter deposited.

Hayes (1957) derived a number called the 'quality index', a theoretical value which was intended to remove the effect of mean depth on production and disclose the inherent productive capacity of a lake, i.e. the amount which a given lake could produce if it were considered as of standard depth of 5 meters. This approach was further refined by Hayes and MacAuley (1959) and Hayes and Anthony (1964).

It is well documented, principally by Deevey (1940), Nygaard (1955), Ohle (1956) and Vinberg (1963) that the rate of primary production per unit surface area is considerably influenced by the morphometric characteristics of lake basins and by water transparency. Consequently, lakes of the same primary trophic state may exhibit wide differences in their rates of primary production per unit surface area, or lakes belonging to different trophic states may have the same rates of primary production per unit surface area, imposed by the differences in their morphometry, water transparency and climate. Deep, clear, oligotrophic or mesotrophic lakes with low or moderately low rates of primary production per unit volume may have rates of primary production per unit surface area similar to or larger than those of shallow, highly coloured eutrophic lakes with high rate of primary production per unit volume. In very shallow bodies of water, primary production per unit surface area is seriously limited by insufficient depth and in highly productive waters increased algal density reduces light penetration thus limiting the depth of the trophogenic zone.

The complicating effects of basin morphometry and water transparency on primary production and on the realized trophic state of bodies of water became obvious in Vinberg's (1963) classification of trophic status of lakes. More than an eightfold variation in areal production in one category and a complete overlap between categories show the limitation of this classification because it cannot separate primary (edaphic) and secondary (physical) trophic characteristics.

Similarly, Rodhe's (1958*a*, 1969) tentative trophic classification is useful to establish the primary trophic state of bodies of water but it gives no allowance for decisive influences such as form of lake basin.

Consideration of only primary production per unit surface area and per unit volume (at optimal light) when making regional comparisons or when evaluating the effective trophic state of individual lakes is inadequate, since the utilization of primary production is dependent on morphometric characteristics (Ohle 1956). Therefore, it is useful to express primary production in a way that would reflect the effect of basin morphometry on production per unit surface area and on its ultimate utilization. This can be achieved if the rate of primary production is expressed on the basis of mean unit volume representative of the whole lake, indicating the availability of primary production to the whole water mass in that basin.

This paper is the third in a series, based on an earlier detailed report (Kerekes, 1972) describing the relationship of limnetic phytoplankton production to physicochemical and morphometric factors in five small lake basins in Terra Nova National Park in Newfoundland.

## METHODS

Soundings of lakes were made with electronic depth recorders. Total inorganic carbon available for photosynthesis was determined from total alkalinity values, pH and temperature (Kerekes 1974), from the table of Bechmann (Saunders et al. 1962).

Radiocarbon procedures are outlined in detail by Kerekes (1974). Samples were incubated in special *in situ* apparatus (Watt 1965) for 3 hours from 1030, suspended at 0, 0.1, 0.5, 1, 2, 3, 4, 5, 7 and 9 m depths. After incubation, measured subsamples of 25 to 40 ml from each bottle were filtered through 24 mm HA Millipore filters, using vacuum below 300 mm Hg to reduce the rupture of fragile algal cells (Arthur and Rigler 1967). The filters then were placed on aluminum planchettes and the activity of the filters was determined with a glas-flow Geiger-Müller counter, having a micromil window.

### *Units of Primary Production*

The units used in expressing planktonic primary production measurements obtained by *in situ* $^{14}C$ experiments in lakes are far from uniform in the prevailing literature and often lead to misinterpretation when the results of different authors are compared. In order to facilitate such comparison, the most commonly used units of primary production rates are defined and presented here, and the units will be used in this study as defined. Surface areas, volumes and depths are given in metric units.

*Primary production per unit volume*

The rates of carbon assimilation for unit volume per unit time may be given as:

1. *Unit volume primary production* (P-vol) at a certain point on the $^{14}C$ production graphic curve or at a given sampling depth 'mgC per $m^3$ per time at depth $z$' (Steeman Nielsen 1952, 1958).
2. *Unit volume maximum primary production* (P-max) when distinct production optimum exists on the $^{14}C$ production graphic curve, 'mgC per $m^3$ max per time'. Curves with maximum primary production at the surface, usually associated with low light intensities, are not considered (Rodhe 1958*b*).
3. *Unit volume euphotic primary production* (P-vol eu) where the value of carbon assimilation in the euphotic zone is divided by the depth of euphotic zone, 'mgC per $m^3$ eu per time' (Goldman 1960).
4. *Unit volume mean primary production* (P-vol $\bar{x}$) where the rates of carbon assimilation at different depths are weighed for the volumes of the same strata and their sum is divided by the total lake volume, 'mgC per $m^3$ $\bar{x}$ per time'. The usage of this new expression is proposed in this study.*

*Primary production per unit surface area*

Rates of carbon assimilation for unit surface area per unit time may be given as:

1. *Unit surface area primary production* (P-area) where the rates of carbon assimilation of unit volume at different depths (mgC per $m^3$ per time at depth $z$) are integrated for a water column in the euphotic zone, 'mgC per $m^3$ per time' (Steemann Nielsen 1952, 1958).
2. *Unit surface area mean euphotic primary production* (P-area $\bar{x}$ eu) where the rate of unit volume euphotic primary production is multiplied by the depth of the euphotic zone or by the mean depth of the body of water, depending upon which value is the lower, 'mgC per $m^2$ $\bar{x}$ eu per time' (Goldman 1960).
3. *Unit surface area mean primary production* (P-area $\bar{x}$) where the rates of carbon assimilation at different depths (mgC per $m^3$ per time at depth $z$) are weighed for the volumes of the same strata, and their sum is divided by the lake surface area or by multiplying the rate of unit volume mean primary production (mgC per $m^3$ $\bar{x}$ per time) by the mean depth of the body of water, 'mgC per $m^2$ $\bar{x}$ per time' (Vinberg 1963).* **

* Kerekes (1973) gives formulas to calculate P-vol $\bar{x}$ and P-area $\bar{x}$.

** Investigators using the dark and light oxygen-bottle method in lakes prior to the introduction of $^{14}C$ utilization (summarized by Vinberg, 1963), considered production both under unit area for the water column in which the actual experiment occurred and under unit surface area where the production values were adjusted to compensate for lake morphometry, in the manner introduced by Strøm (1931) for calculations of oxygen deficit. This latter practice, however, was not accepted by the majority of investigators using $^{14}C$ utilization.

## RESULTS

The five lakes investigated are located in Terra Nova National Park in north-eastern Newfoundland between 53°41′ and 54°14′ west longitudes and between 48°23′ and 48°40′ north latitudes. The morphometric and physicochemical characteristics of the five lakes are given by Kerekes (1974*a*). The hypsographic curves show the relationship of various depths to surface area (Fig. 1). The mean depths range from 1.06 m (Pine Hill Pond) to 9.23 m (Bluehill South Pond), maximum depths range from 5.5 m to 22.6 m, respectively.

The hourly rates of P-max, P-area, P-area $\bar{x}$, P-vol $\bar{x}$ for the growing season, and the probability test for 'U' for the Wilcoxon two sample test of ranked observations (Sokal and Rohlf 1969) are summarized in Tables 1 to 4. The P-area $\bar{x}$ rates expressed as percentage of P-area are given in Table 5.

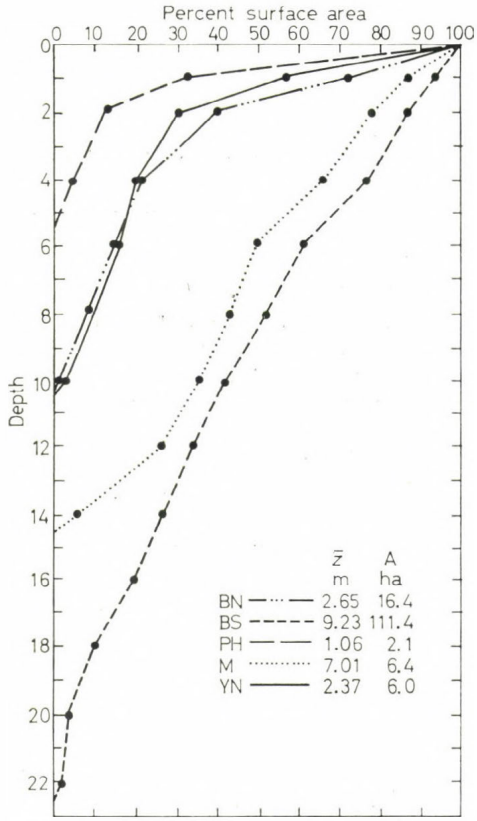


Fig. 1. Hypsographic curves in Bluehill North (BN), Bluehill South (BS), Pine Hill (PH), Minchin (M) and Yudle North (YN) Ponds in Terra Nova National Park, Newfoundland. Mean depth ($\bar{z}$) in metres and lake surface area (A) in hectares are given in the legend

## DISCUSSION

### *Production Optimum (P-max)*

The primary production per unit volume at optimum light (P-max) is particularly valuable for the biological characterization of different waters regarding their primary trophic state (Rodhe, 1958*a*, *b*). Rodhe came to this conclusion after examining the primary production in a large number of lakes ranging from oligotrophic to highly eutrophic lakes in several geographic regions. He found that P-max is a better indicator of the trophic status of a lake than P-area, because the former is not dependent on the depth of the productive zone.

Based on the P-max values, Pine Hill Pond had the most productive water in this study because both the mean and the maximum P-max values were the highest among the five lakes, while Bluehill South Pond had the least productive water (Table 1). The P-max values in Pine Hill Pond were significantly higher ($p = 0.05$ to $p < 0.002$) than that in any of the other lakes except in Minchin Pond, which had the second highest P-max value, and they were significantly lower ($p < 0.01$ to $p < 0.002$) in Bluehill South Pond than that in the other lakes, except in Bluehill North Pond which had the second lowest mean P-max value. The $^{14}C$ experiments were con-

TABLE 1

*Hourly primary production per unit volume at optimum light (P-max) between May and October 1969 and May and August, 1970, in five study lakes in Terra Nova National Park, Newfoundland, and probability test for 'U' for the Wilcoxon two-sample test of ranked observations. Days with P-max at the surface are excluded*

| Pond | mgC/m³ max/h | | No. of observations |
|---|---|---|---|
| | Mean | Range | |
| Bluehill South | 0.96 | 0.27–1.65 | 10 |
| Bluehill North | 1.39 | 0.48–2.85 | 10 |
| Yudle North | 1.63 | 0.87–2.19 | 11 |
| Minchin | 1.89 | 0.96–4.09 | 9 |
| Pine Hill | 2.66 | 0.68–5.94 | 18 |

*Probability test for 'U'*

| Pond | BS | BN | YN | M | PH |
|---|---|---|---|---|---|
| BS | — | | | | |
| BN | $p < 0.2$ | — | | | |
| YN | $p < 0.01$* | $p < 0.2$ | — | | |
| M | $p < 0.02$* | $p < 0.2$ | $p > 0.2$ | — | |
| PH | $p < 0.002$* | $p < 0.02$* | $p = 0.05$* | $p < 0.2$ | — |

* Significant difference

ducted simultaneously in Bluehill South and Bluehill North Ponds and on any given day the P-max values obtained were almost always higher in Bluehill North Pond. In spite of the trend toward higher P-max values on individual days and the higher mean P-max value in Bluehill North Pond, the ranked P-max values in the two lakes were not significantly different. Similarly, when the lakes were listed in the order of increasing mean P-max values the differences in P-max values between two adjacent lakes were not significantly different.

### *Areal Production (P-area)*

The five lakes are oligotrophic based on their primary production rates of unit surface area (P-area), according to the scheme of classification proposed by Rodhe (1969). The ranked P-area values during the ice-free period were significantly higher ($p < 0.01$) in Pine Hill Pond than in any of the other four lakes (Table 2). No significant differences in P-area values existed among those lakes. The relatively high mean P-area in Pine Hill Pond was the consequence of higher rates of P-vol. This was exemplified by the highest P-max value and the frequent occurrence of two production maxima on the vertical distribution of planktonic production (Kerekes 1974*b*). In the remaining four lakes the differences in the P-max values were

TABLE 2

*Hourly primary production per unit surface area at the sampling station (P-area) between May and October, 1969 and May and August, 1970 in five study lakes in Terra Nova National Park, Newfoundland, and probability test for 'U' for the Wilcoxon two-sample test of ranked observations*

| Pond | mgC/m²/h | | No. of observations |
|---|---|---|---|
| | Mean | Range | |
| Bluehill North | 3.01 | 0.83– 6.64 | 13 |
| Bluehill South | 3.02 | 0.84– 6.29 | 15 |
| Yudle North | 3.41 | 0.76– 6.68 | 17 |
| Minchin | 3.78 | 1.15– 8.69 | 13 |
| Pine Hill | 6.39 | 0.87–19.48 | 25 |

*Probability test for 'U'*

| Pond | BS | BN | YN | M | PH |
|---|---|---|---|---|---|
| BS | — | | | | |
| BN | $p > 0.2$ | — | | | |
| YN | $p > 0.2$ | $p > 0.2$ | — | | |
| M | $p > 0.2$ | $p > 0.2$ | $p > 0.2$ | — | |
| PH | $p < 0.01$* | $p < 0.01$* | $p < 0.01$* | $p < 0.01$* | — |

* Significant difference

not reflected in the respective P-area values which were the most obvious in Bluehill South and Minchin Ponds. The mean P-max value (1.89 mgC per $m^3$ max per h) in Minchin Pond was almost twice of that in Bluehill South Pond. The ranked P-max values were significantly different at the level of $p < 0.02$, yet the mean P-area in Minchin Pond was only 25 per cent higher than that in Bluehill South Pond, and the ranked values of P-area in these two lakes were not significantly different in spite of the greater number of samples in P-area from both lakes, as compared to the number of P-max values. The reduced light penetration resulting from the relatively high water colour caused unfavourable conditions for area production in Minchin Pond, partly because the depth of the euphotic zone was considerably reduced and also because of the increased vertical light extinction. Light itself became progressively more limiting with increase in depth so that rates of P-vol declined rapidly below P-max (Talling 1961, 1965). As a result, Minchin Pond, which was considered more productive than Bluehill South Pond based on their P-max values, did not have significantly higher P-area rates than those in Bluehill South Pond, because in the latter the deeper euphotic zone and the relatively moderate decline of P-vol below P-max compensated for the lower P-max rates. For the same reason, mean P-area values were identical in Bluehill South and Bluehill North Ponds in spite of the different P-max rates in the two lakes.

### *Euphotic Production (P-area $\bar{x}$ eu)*

Goldman (1960) recognized the inadequacy of using P-area as the basis for meaningful comparison of primary production among lakes on the basis of unit surface area. However, his proposal which has been accepted by some authors (Narver 1967, Kalff 1967), to use P-area $\bar{x}$ eu for the correction of the shape of basin on P-area, fell short of its intended purpose, particularly for shallow lakes. It misrepresents areal production which should be expressed as P-area $\bar{x}$ (Vinberg 1963).

### *Unit Area (P-area $\bar{x}$) and Unit Volume (P-vol $\bar{x}$) Production*

The P-area gives an increasingly misleading representation of the true areal planktonic primary production (P-area $\bar{x}$) as the mean depth decreases because in more shallow lakes the depth of the euphotic zone is drastically reduced over a large portion or the whole basin because of insufficient depth.

The relationship between the logarithm of mean depth in metres and the logarithm of mean rates of P-area $\bar{x}$ and P-vol $\bar{x}$ expressed as percentages of P-area during the ice-free period in the five lakes is shown in Fig 2. The graph suggests, mean depth reduces P-area $\bar{x}$ as compared to P-area when mean depth is approximately 12 m or less. Then, P-area $\bar{x}$ becomes progressively smaller when expressed as percentage of P-area with decrease in mean depth. However, at the depth at which P-area $\bar{x}$ begins to decline, P-vol $\bar{x}$ continues to increase with decrease in mean depth but at a reduced rate.

The heavy broken lines in Fig. 2 indicate the theoretical relationship when the effect of basin morphometrics is absent on areal production, i.e. when maximum depth and mean depth are equal. Then the relationship between P-vol $\bar{x}$, P-area and mean depth can be described as $\log y = \log 2 - \log x$

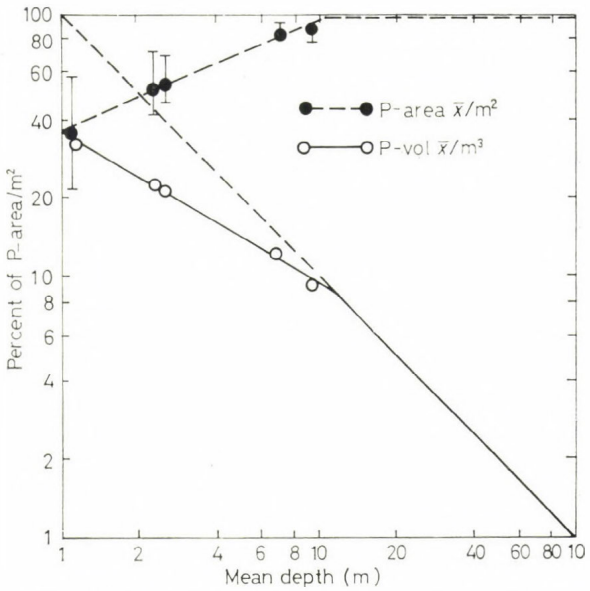


Fig. 2. The relationship between areal primary production (P-area and P-area $\bar{x}$) and unit volume primary production (P-vol $\bar{x}$) in five lakes, varying in mean depth, in Terra Nova National Park, Newfoundland. Solid and open circles represent the average P-area $\bar{x}$ and P-vol values, respectively, expressed as percentages of P-area for the ice-free study period in 1969 and 1970. The vertical bars show the range of values for P-area $\bar{x}$ for the same period

where $y$ = P-vol $\bar{x}$ expressed as percentage of P-area and $x$ = mean depth. Under this condition, areal production, either P-area or P-area $\bar{x}$ are equal at all mean depths, both having 100 per cent value at all mean depths. When mean depth equals one meter, then P-vol $\bar{x}$ becomes equal to P-area, and when it is less than one meter, P-vol $\bar{x}$ will be greater than P-area.

To demonstrate the effect of light penetration (depth of euphotic zone) on P-area $\bar{x}$ in the study lakes, a series of calculations was performed in which the P-vol obtained in one lake during the ice-free period were used to calculate P-area $\bar{x}$ expressed as percentage of P-area utilizing the morphometric data for each of the other four lakes. Figure 3 depicts the two extreme regressions obtained from these calculations. The upper line is the regression with the smallest percentage loss in P-area based on primary production rates obtained in Minchin Pond which has the most coloured water and the smallest variation in water colour among the study lakes. The lower line shows a similar relationship, but with considerably greater percentage losses in P-area using the P-vol obtained in Bluehill South Pond which has the least coloured water and the deepest euphotic zone among

the five lakes. The regressions calculated in a similar fashion for the other three lakes (not shown on the graph) were between the two lines described. The third regression presents the actual relationship of P-area $\bar{x}$ and mean depth in the five lakes (Table 5). The graph shows that at the same mean depth the percentage loss in P-area is greater, and that loss is increasing at a faster rate with a decrease in mean depth, when the vertical light extinction is smaller.

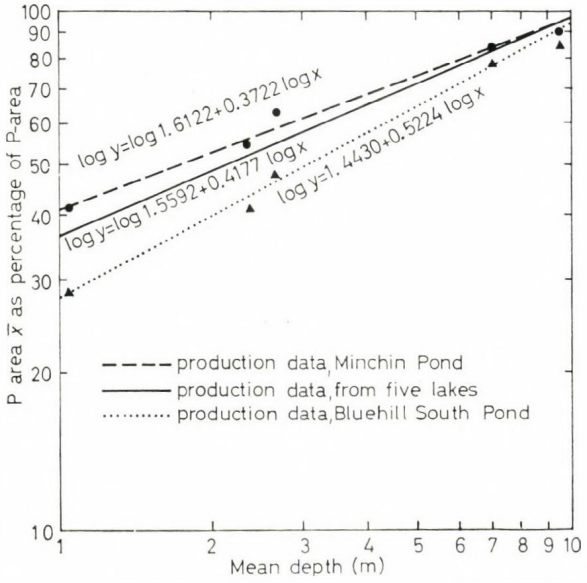


Fig. 3. The effect of light penetration on P-area $\bar{x}$, expressed as percentage of P-area in Bluehill North, Bluehill South, Minchin, Pine Hill and Yudle North Ponds in Terra Nova National Park, Newfoundland. The regression line at the centre, indicated by solid line, is based on the mean P-area $\bar{x}$ values of the five lakes studied (Fig. 2). The upper regression line is based on P-area $\bar{x}$ values (solid circles) calculated from the P-vol rates of Minchin Pond (most coloured lake) for each lake. The P-vol rates of Bluehill South Pond (least coloured lake) were used to fit the lower regression line

As expected from Fig. 2, the mean P-area $\bar{x}$ values were the highest in the deepest lakes and the rank position of the five lakes was considerably different from that of the mean P-area values (Tables 2–3). Pine Hill Pond, which had the lowest mean depth, suffered the greatest percentage loss in P-area value. The influence of mean depth on P-area $\bar{x}$ may be best examined in Bluehill South and Bluehill North Ponds, where the $^{14}C$ experiments were conducted simultaneously, presumably under identical light intensities at the surface. The mean P-area values were identical in these two lakes but after correction for basin shapes the mean P-area $\bar{x}$ value was 50 per cent higher in the deeper Bluehill South Pond but the difference between the ranked observations was not significant.

The autotrophy of a lake (Åberg and Rodhe 1942) depends upon the depth of the euphotic zone but its utilization through secondary and tertiary production and its ultimate mineralization depend on the whole water

TABLE 3

*Hourly primary production per unit surface area, representative for the basin (P-area $\bar{x}$) between May and October, 1969 and May and August, 1970 in five study lakes in Terra Nova National Park, Newfoundland, and probability test for 'U' for the Wilcoxon two-sample test of ranked observations*

| Pond | mgC/m² $\bar{x}$/h | | No. of observations |
|---|---|---|---|
| | Mean | Range | |
| Yudle North | 1.67 | 0.44–2.96 | 17 |
| Bluehill North | 1.67 | 0.56–3.94 | 13 |
| Pine Hill | 1.98 | 0.48–5.25 | 25 |
| Bluehill South | 2.57 | 0.74–5.29 | 15 |
| Minchin | 3.20 | 0.99–7.29 | 13 |

*Probability test for 'U'*

| Pond | YN | BN | PH | BS | M |
|---|---|---|---|---|---|
| YN | – | | | | |
| BN | $p > 0.2$ | – | | | |
| PH | $p < 0.4$ | $p < 0.5$ | – | | |
| BS | $p < 0.1$ | $p < 0.2$ | $p < 0.4$ | – | |
| M | $p < 0.01$* | $p < 0.01$* | $p < 0.05$* | $p > 0.2$ | – |

* Significant difference

mass (Ohle 1956). Consideration of autotrophy and the modifying influence of morphometric characteristics of lake basins made trophic classification of lakes excessively complex as has been exemplified by the proposed system of Järnefelt (1958). Rodhe (1958*a*, 1969) is of the opinion that all differentiation except those of oligotrophy and eutrophy should be abandoned and that the degree of oligotrophy or eutrophy must be measured at the level of primary production. Other characteristics of lakes such as morphometrics and physicochemical conditions should be defined and compared separately.

The influence of mean depth on the availability of primary production for secondary producers or for decomposition may be expressed simply as P-vol $\bar{x}$, which could be used for the comparison of effective trophic state of different water bodies, irrespective of their volumes and mean depths.

The ranked P-vol $\bar{x}$ rates were significantly different ($p < 0.02$) among the five lakes except between Yudle North and Bluehill North Ponds and Bluehill North and Minchin Ponds where the differences between the means were not significant (Table 4). The largest P-vol $\bar{x}$ rates were the highest in the shallow Pine Hill Pond, and the ranked rates were different at a very high level of significance ($p < 0.001$) from the ranked rates in the other four lakes, suggesting that the effective trophic state of Pine Hill Pond was nearly eutrophic, while the deepest lake, Bluehill South Pond, was the most oligotrophic.

TABLE 4

*Hourly primary production per unit volume representative for the basin (P-vol $^{-}$) between May and October, 1969 and May and August, 1970 in five study lakes in Terra Nova National Park, Newfoundland, and probability test for 'U' for the Wilcoxon two-sample test of ranked observations*

| Pond | mgC/m³ $\bar{x}$/h | | No. of observations |
|---|---|---|---|
| | Mean | Range | |
| Bluehill South | 0.28 | 0.08–0.57 | 15 |
| Minchin | 0.46 | 0.14–1.04 | 13 |
| Bluehill North | 0.64 | 0.21–1.50 | 13 |
| Yudle North | 0.70 | 0.19–1.25 | 17 |
| Pine Hill | 1.87 | 0.45–4.95 | 25 |

*Probability test for 'U'*

| Pond | BS | M | BN | YN | PH |
|---|---|---|---|---|---|
| BS | – | | | | |
| M | $p = 0.02$* | – | | | |
| BN | $p < 0.002$* | $p < 0.20$ | – | | |
| YN | $p < 0.001$* | $p = 0.02$* | $p > 0.20$ | – | |
| PH | $p < 0.001$* | $p < 0.001$* | $p < 0.001$* | $p < 0.001$* | – |

* Significant difference

TABLE 5

*P-area $\bar{x}$ expressed as percentage of P-area during the ice-free period between April, 1969 and August, 1970 in five lakes studied in Newfoundland*

| Pond | P-area $\bar{x}$ P-area · 100 | | No. of observations |
|---|---|---|---|
| | Mean | Range | |
| Pine Hill | 35.45 | 21.2–59.0 | 28 |
| Yudle North | 52.71 | 40.5–71.3 | 20 |
| Bluehill North | 57.27 | 46.3–69.6 | 14 |
| Minchin | 85.30 | 81.0–89.6 | 15 |
| Bluehill South | 85.90 | 79.9–91.0 | 17 |

The inadequacy of comparing lakes based on P-area alone is obvious from the figures in Table 6. Crater Lake (Larson 1970), for example, has a P-max of 0.4 mgC per m³ max per h, thus it can be described as an extremely oligotrophic lake but because it has an unusually deep euphotic zone (200 m), its P-area rates reach 225 mgC per m² per day, thus according to Rodhe (1969) it should be considered as moderately eutrophic. A similar anomaly was found in Lake Superior which also had low P-max rates but P-area rates that averaged 185 mgC per m² per day during the growing season (Parkos et al. 1969).

TABLE 6

*Hourly rates of primary production measured with $^{14}C$ technique in some lakes of different geographical areas in midsummer*

| Lake | mg Carbon | | | Reference |
|---|---|---|---|---|
| | $m^3$ max/h | $m^2$/h | $m^3$ $\bar{x}$/h | |
| Bluehill North (Newfoundland) | 2.0 | 4.7 | 0.7 | This study |
| Bluehill South (Newfoundland) | 1.7 | 6.3 | 0.5 | This study |
| Minchin (Newfoundland) | 4.1 | 7.3 | 0.8 | This study |
| Pine Hill (Newfoundland) | 4.5 | 13.6 | 3.0 | This study |
| Yudle North (Newfoundland) | 2.2 | 6.7 | 0.9 | This study |
| Dunlop (Ontario) | 2.5 | 12.6 | — | Johnson et al. (1970) |
| Nanek (Alaska) | 1.4* | 16.7* | — | Goldman (1960) |
| Torne Trask (Lappland) | 0.8** | — | — | Rodhe (1958*a*) |
| Ransaren (Lappland) | 1.1** | — | — | Rodhe (1958*a*) |
| Marion (British Columbia) | 3.0 | — | — | Dickman (1969) |
| Superior (Ontario) | 0.7 | 18.0* | 0.12* | Olson and Odlaug (1966) |
| Crater (Oregon) | 0.4 | 21.4 | 0.07* | Larson (1970) |
| Weldo (Oregon) | 0.4 | 5.1 | — | Larson (1970) |
| Odell (Oregon) | 30.0 | 223.0 | — | Larson (1970) |
| 305 (Ontario) | 14.2* | 85.0* | — | Schindler and Holmgren (1971) |
| East Winnipeg (Manitoba) | 3.0* | 5.0* | — | Schindler and Holmgren (1971) |
| Great Slave (N. W. Territories) | 0.2* | 10.0* | — | Schindler and Holmgren (1971) |
| Esrom (Denmark) | 93.0* | 151.0* | — | Jonasson and Kristiansen (1967) |
| Babine (British Columbia) | — | 10.2 | — | Narver (1967) |
| Owienko (British Columbia) | — | 7.6 | — | Narver (1969) |
| Valkiajarvi (Finland) | 3.0* | 15.0* | — | Meriläinen (1970) |
| Tahoe (California) | 0.2 | 70.0 | — | Goldman (1960) |
| Cedar (California) | 2.3 | 6.0 | — | Goldman (1960) |

* Estimated.
** Upward correction by 45 percent (Goldman, 1968) not included.

Hourly P-vol $\bar{x}$ rates for Crater Lake and Lake Superior were calculated by dividing P-area with the mean depth, a permissible procedure in these two lakes because of their great mean depths. The rates obtained for P-vol $\bar{x}$ for these two deep lakes are considerably lower, by an order of magnitude in some instances, for Crater Lake, compared to my five lakes, suggesting clearly a much greater degree of oligotrophy in the deep lakes in spite of their higher areal production.

It is obvious that a single and simple system of classification of lakes and basin-lake systems is not feasible. Several factors such as P-max, P-area $\bar{x}$, $k_b$ (biological extinction coefficient; Platt 1969), nutrient supply, water renewal rate should be considered to assess the trophic status of a lake or catchment area-lake system. It is proposed that P-vol $\bar{x}$ should be used as a relative index of the effective trophic status of a lake. The P-vol $\bar{x}$ with the other indices of trophic status would provide an effective tool to define the trophic status and to evaluate the effect of artificial enrichment of lakes.

*

*Acknowledgements.* I acknowledge my gratitude to Mr. J.-P. Cuerrier, Canadian Wildlife Service, who has provided help, ideas and continuous encouragement during this study. I am much indebted to Mr. P. Schwinghamer for providing excellent assistance in various phases of this project, to Dr. P. J. Bhattacharyya for computer programming assistance, to Drs D. R. Flook and E. T. Garside for comments on the manuscript.

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*Symp. Biol. Hung.*, *15*, pp. 49–62 (1975)

# PRIMARY PRODUCTIVITY IN THE LITTORAL ZONE OF LAKE TAHOE, CALIFORNIA-NEVADA

by

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## INTRODUCTION

Lake Tahoe lies at an altitude of 1898 m in the Sierra Nevada. It is a large (499 km$^2$), deep, subalpine lake, formed in a graben fault, with a maximum depth of 501 m. The lake basin has steep sides, a flat bottom, and very little shallow water for its size (Fig. 1). The average depth of the lake is 313 m and its shoreline covers 113 km. Lake Tahoe is particularly renowned among the lakes of the world for its great transparency and the beauty of its deep blue colour (Smith et al. 1973). Mean monthly Secchi depth readings

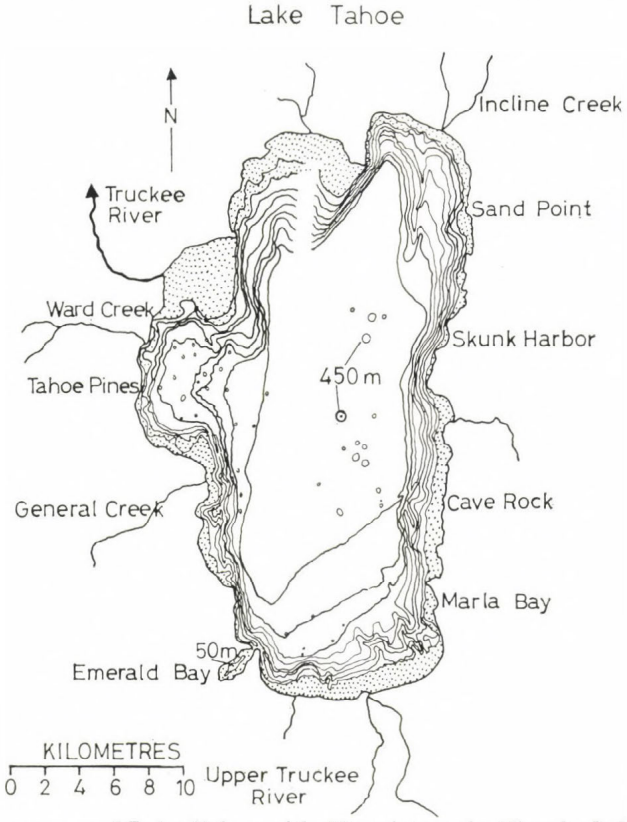


Fig. 1. Contour map of Lake Tahoe with 50 m intervals. The shaded area indicates the littoral zone which extends down to 100 m

greater than 35 m have been recorded in the winter months and the compensation depth is measured close to 105 m. In such a clear lake, the littoral zone extends to a depth of 100 m, representing only 18.7 per cent of the surface area of the lake. This narrow band of shallow water has, however, great importance to the many users of the lake and provides the main visual evidence of water quality to the largely shore-bound populace.

Primary productivity of phytoplankton in this extremely oligotrophic lake is only a few mgC $m^{-3}$ $day^{-1}$ and its biomass ranges from 10 to 100 mg fresh weight per $m^3$. The phytoplankton population is very diverse with over 160 species. Eighty-six species of periphyton have been identified so far in the lake (Table 1). As expected, some of the periphyton also occur in the phytoplankton.

The substrata in the littoral zone varies from fine sand to boulders. The surface water temperature ranges from 4.6 °C in the winter to 19 °C in the summer. Levels of nitrate, total phosphorus, and iron are very low all year round (less than 10 $\mu g\ l^{-1}$). In contrast, levels of silicon, so important for maintaining diatom populations, are of the order of 3 to 7 mg $l^{-1}$ $SiO_3^=$-Si.

There are only a few isolated beds of macrophytes (*Anachous canadensis*, *Myriophyllum* sp., *Potomogeton crispus*) in the littoral zone of the lake with an abundance of chara, the fungus *Apostemidium guernisal*, and aquatic moss (Fissidens), together with luxuriant growths of filamentous periphyton extending to depths of about 100 m (Frantz and Cordone 1967). No attempt has been made in this report to estimate the abundance or productivity of these higher and lower plants.

## METHODS

Periphyton was studied in 1971 at 17 stations around the lake. Each offshore station consisted of a wooden rack anchored to the bottom of the lake in 10 m of water (Fig. 2). The rack was held in place 5 m above the bottom by submerged floats. The station location was determined by triangulation on terrestrial landmarks. Pyrex®glass tubing cylinders, used as substrates for periphyton growth, were held by test tube holders attached to the rack. Installation and retrieval of the cylinders were done by SCUBA. Four samples were collected for each growth period. Three samples for total carbon measurement were placed in polyethylene vials and kept frozen until analysis. The fourth sample was placed in a glass vial filled with distilled water and fixed with Lugol's solution for periphyton species identification and enumeration.

A rapid method for the estimation of the carbon content in periphyton (Armstrong et al. 1971) was used to determine the amount of organic carbon that accumulated on the cylinder during the growth period. The method consists of combusting the sample in an induction furnace and measuring the evolved carbon as $CO_2$ with an infrared gas analyser.

Preparation of the sample for periphyton identification and enumeration was initially accomplished by scraping the periphyton off the cylinder into its glass vial container. Later in the study, removal of periphyton from the cylinder was greatly facilitated by placing the glass vial containing the cylinder in an ultrasonic cleaner for five minutes. The sample was then

TABLE 1

*Lake Tahoe periphyton. Periphyton species list compiled from microscopic examination of live and preserved samples on glass cylinders and rocks. Where cell volumes have been measured they are given in ($\mu^3$)*

CHLOROPHYCEAE
- *Sphaerocystis schroeteri* (268)
- *Geminella ordinata*
- *Ulothrix* sp.
- *Bulbochaete* sp.
- *Pediastrum sculptatum*
  - *tetras* var. *tetradon*
- *Mougeotia genuflexa*
- *Spirogyra* sp.
- *Zygnema* (sterile)
- *Cosmarium* sp. a
  - sp. b
- *Euastrum bidentatum*
- *Pleurotaenium* sp.
- *Straurastrum natator* (4350)

EUGLENACEAE
- *Euglena* sp.

DINOPHYCEAE
- *Peridinium pusillum*

CHRYSOPHYCEAE
- *Dinobryon sertularia* (900)

BACILLARIOPHYCEAE
- *Cyclotella antigua* (635)
  - *bodanica* (4778)
- *Melosira crenulata* (1209)
  - *varians* (4301)
- *Stephanodiscus astrea* (707)
- *Diatomella balfouriana* (660)
- *Tabellaria flocculosa* (2700)
- *Diatoma anceps* (1000)
  - *hiemale* (*mesodon*) (1060)
  - *vulgare* (3600)
- *Opephora americana*
- *Asterionella formosa* (480)
- *Fragilaria capucina* (140)
  - *crotonensis* (510)
  - *intermedia* (2500)
  - *pinnata* (175)
  - *vaucheriae* var. *capitellata* (276)
- *Synedra actinastroides*
  - *ulna* (19 200)
  - *ulna spathulifera*
- *Eunotia tenella* (590)
- *Achnanthes clevei* (350)
  - *flexella* (880)
  - *lanceolata* (420)

BACILLARIOPHYCEAE (contd.)
- *Achnanthes microcephala*
  - *peragalli* (430)
- *Cocconeis placentula* (503)
- *Amphipleura pellucida* (4080)
- *Diploneis elliptica* (1781)
  - *oculata* (330)
- *Frustulia rhomboides* (7600)
- *Mastogloia smithii* (5184)
- *Navicula aurora* (14 016)
  - *bacillum* (2000)
  - *cocconeiformis* (980)
  - *elginensis*
  - *pupula* (1000)
  - *radiosa* (1100)
- *Neidium hitcheockii* (14 800)
- *Pinnularia biceps* (4980)
  - *rupestris* (18 000)
- *Gomphoneis herculeana* (6831)
- *Gomphonema acuminatum* (610)
  - *parvulum* (350)
- *Amphora ovalis* (2500)
- *Cymbella cuspidata* (10 000)
  - *lanceolata* (6000)
  - *prostrata* (15 750)
  - *sinuata* (375)
  - *ventricosa* (1800)
- *Epithemia argus*
  - *sorex* (5125)
  - *turgida* (66 000)
  - *zebra* (11 520)
- *Rhopalodia gibba* (8000)
- *Denticula (elegans)*
- *Nitzschia linearis*
  - *(sigma?)*
- *Cymatopleura solea* (var?) (37 370)
- *Surirella (didyma)* (13 000)

CYANOPHYCEAE
- *Oscillatoria tenuis*
- *Anabaena (variabilis?)*
- *Nostoc microscopicum*
- *Calothrix parietana*
- *Scytonema myachrous*
- *Lyngbya nordgardii*
- *Nephrocytium agardhianum*
- *Tolypothrix* sp.

CRYPTOPHYCEAE
- *Cryptomonas reflexa?*

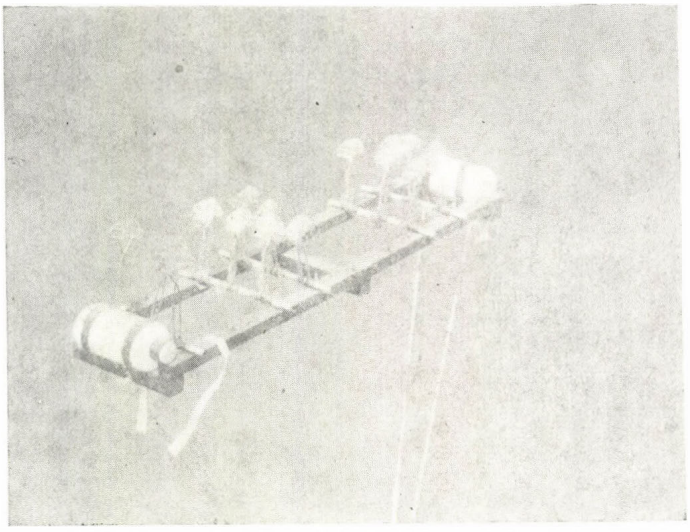

Fig. 2. Underwater picture of the wooden rack at the periphyton station, with the glass tubing cylinders held by test tube holders. Four floats hold the station in place 5 m above the bottom

shaken well to insure uniform distribution of the cells, a subsample was settled in an Utermöhl chamber, and identification was done using a Wild M-40 inverted phase microscope.

Preliminary periphyton species identification was done from live samples, using glass cylinders that had been exposed at locations around the lake for 14 weeks between 24 June 1970 and 30 September 1970. The influence of the substrate on species composition was investigated by comparing glass cylinders and natural rock communities at several locations. Communities from both fresh and preserved samples on glass cylinders were compared at several locations to determine the effect of preservation.

Samples from some of the major tributaries to the lake were also examined for species composition.

## RESULTS

### *Periphyton taxonomy*

Observations made on the cylinders incubated for 14 weeks during the summer of 1970 are shown in Fig. 3. One Chlorophycean species (*Mougeotia genuflexa*) and six diatoms were found to be the dominant species. *Mougeotia genuflexa* occurred at all stations. Cylinders off the south-southeast shore of the lake were invaded by a relatively few (three or four) dominant species in comparison to the other stations (six dominant species), but their growth coverage was dense or very dense. Emerald Bay, which is partially isolated from the rest of the lake, had seven dominants. *Fragilaria capucina* was a dominant form only off the Upper Truckee River mouth and in Emerald Bay.

Results shown in Fig. 4 are based on observations made on four to eight different samples at each station. These samples had been left in the lake for lengths of time varying from two weeks to 23 weeks (overwinter) between 1 October 1970 and 2 May 1971. A rating system was devised to determine which species were dominant overall during the season at each sampled location. At each of the stations, for each sample available, the dominant

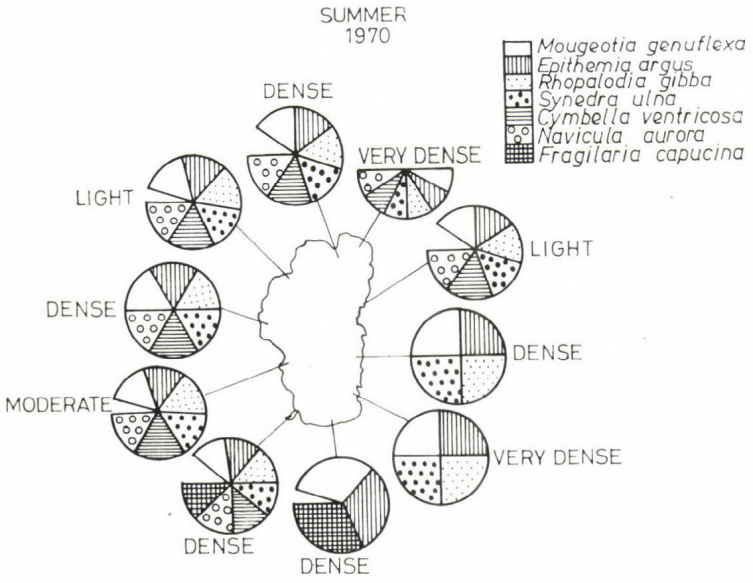


Fig. 3. Dominant species of periphyton found on glass cylinders exposed *in situ* to periphyton invasion for 14 weeks between 24 June 1970 and 30 September 1970. The per cent of the circle drawn represents the percentage of the slide that was covered by periphyton (50, 90, 95 or 100 per cent). The relative density of growth is also indicated

species (dominant in number of cells present) were given a number of points in decreasing order of dominance (10 for the most dominant, 9 for the next dominant, 8 for the next, etc.). The total number of points for each species was computed, and the species that were most dominant during the season determined. The dominant species were those species that received a total number of points 25 per cent or greater of the maximum total possible.

In winter, the number of dominant periphyton species remained substantially unchanged from those in the summer, yet the species composition changed almost completely (Fig. 4). The lake periphyton, in this winter–spring period, was dominated by seven diatom species. *Synedra actinastroides* was the most dominant at all stations. *Fragilaria crotonensis* was the second most dominant species, which was also found at all stations. The same pattern of low diversity (three or four species) that was observed in the summer persisted in the winter along the south-southeast shore. This zone is strongly influenced by the Upper Truckee River (Paerl and Goldman 1972). Some of the dominant species for these seasons are shown in Fig. 5.

Observations of natural communities growing on rocks and piers near the offshore locations during our study of the shallower portion of the littoral zone showed, in addition, a dominance of *Ulothrix* in many of the areas around the lake and *Gomphonema* in some of them. *Ulothrix* is present in a number of tributaries.

Our preliminary comparison of communities growing on glass cylinders and communities growing on natural rocks seemed to evidence better blue-

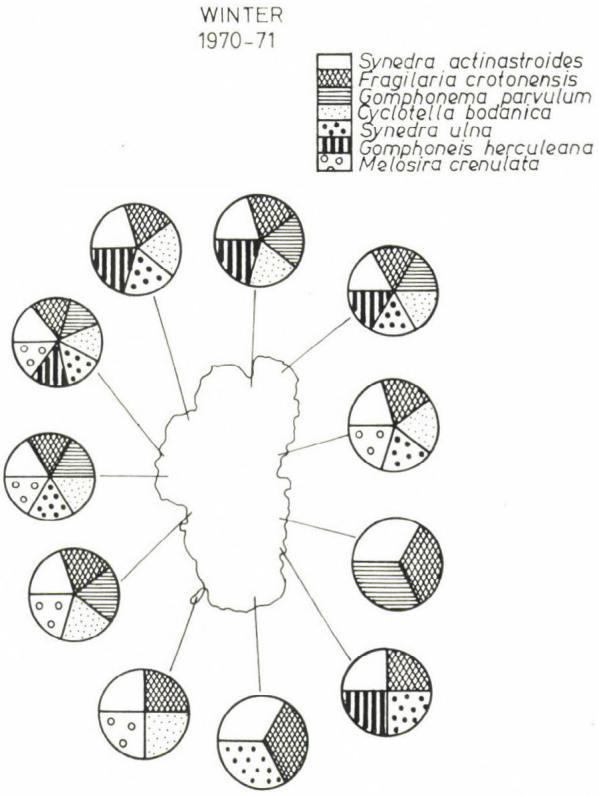


Fig. 4. Dominant species of periphyton found on glass cylinders exposed *in situ* to periphyton invasion for lengths of time varying from two weeks to 23 weeks (over winter) between 1 October 1970 and 2 May 1971

green growth (*Calothrix*, *Tolypothrix*, *Nostoc*) on rocks and better green growth (*Mougeotia*, *Zygnema*, *Spirogyra*) on glass, while diatoms grew well on either substrate. Later study indicated that glass was readily colonized by a large variety of algae. It was felt that rather than the substrate difference, differences in depth, current, and light were primarily responsible for the observed difference in colonization. Fresh samples were essential for accurate identification to the species level and Lugol's solution was found adequate as a preservative for subsequent enumeration.

Periphyton growth around the margins of the lake was measured at the submerged stations described in Methods. Since each was located offshore at a depth of 10 m, the distance from the shore was quite variable. The

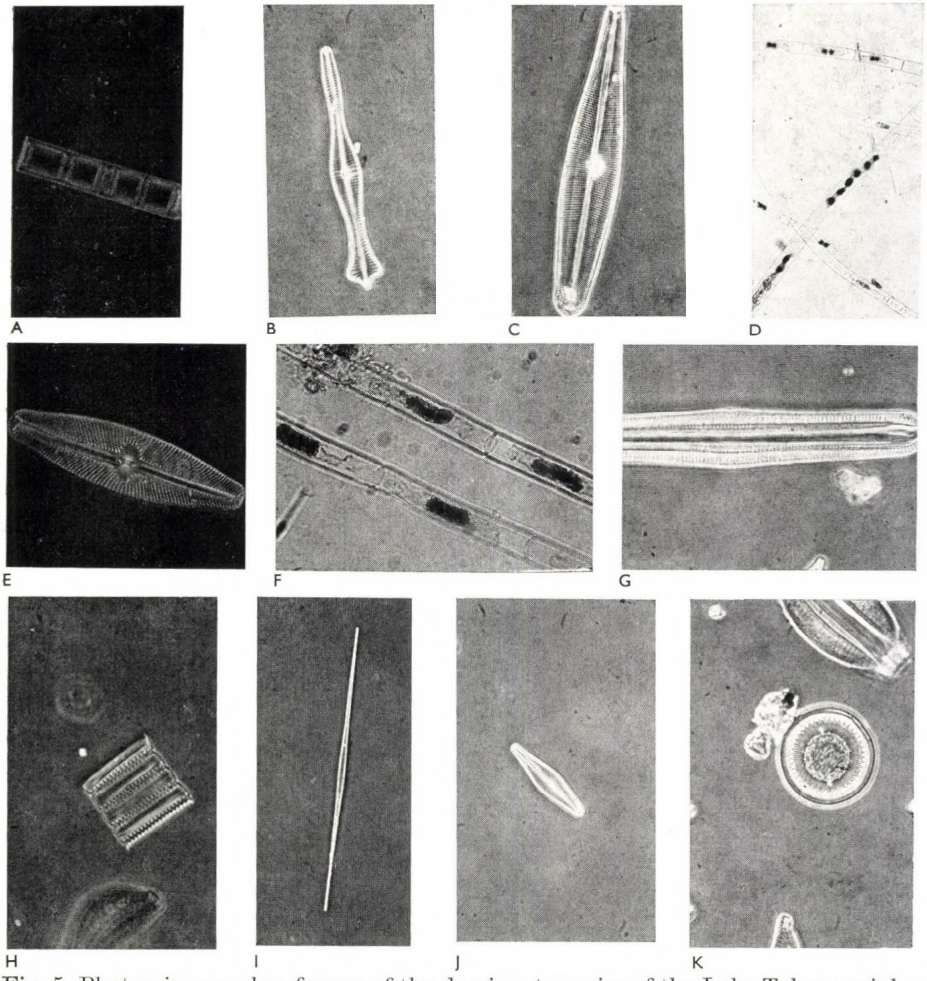


Fig. 5. Photomicrographs of some of the dominant species of the Lake Tahoe periphyton community. The photographs were taken with a Polaroid camera attached to an inverted microscope. Cleared diatom frustules from permanent mounts and other algae from settling chambers were used. The species shown are A, *Melosira crenulata* ×750; B, *Gomphonema acuminatum* ×750; C, *Gomphoneis herculeana* ×750; D, *Zygnema* ×187.5; E, *Navicula aurora* ×750; F, *Mougeotia genuflexa* ×375; G, *Rhopalodia gibba* ×750; H, *Fragilaria pinnata* ×750; I, *Synedra ulna* ×375; J, *Gomphonema parvulum* ×750; K, *Cyclotella bodanica* ×750

highest growth rates were recorded near stream mouths where human activity is greatest, except in the vicinity of the largest tributary, the Upper Truckee River (Fig. 6). The shallow shelf there necessitated placement of periphyton stations 700 to 1200 m from the stream mouth to avoid loss of stations. This remote placement was not necessary off Ward Creek which, together with the Incline Creek location, partially contained by Crystal Bay, showed the highest increments of growth. In general, slower growth occurred in areas of least tributary influence such as along the sparsely populated east shore.

The total production of periphyton per day for the entire littoral zone of Lake Tahoe was estimated by using the results from growth per day at each station as measured in carbon per square metre. Each station was chosen to be representative of a section of the littoral zone delimited by the shoreline, the depth of 100 m, and the distances halfway to the next stations. The periphyton production for that section was obtained by multiplying the surface area (determined by planimetry) by the amount of production at the corresponding station. The sum of the production of these sections gave the estimate of the total production of periphyton per day for the lake. This calculation was done for each of the dates in 1971 for which we had data available from periphyton cylinders left in the lake for a period of 14 days. The results plotted against time are shown in Fig. 7. The growth rate increased steadily from early April until mid-May, levelled out through mid-June, and then declined through mid-July. This follows closely both the seasonal light curve and the influx of nutrients from the watershed.

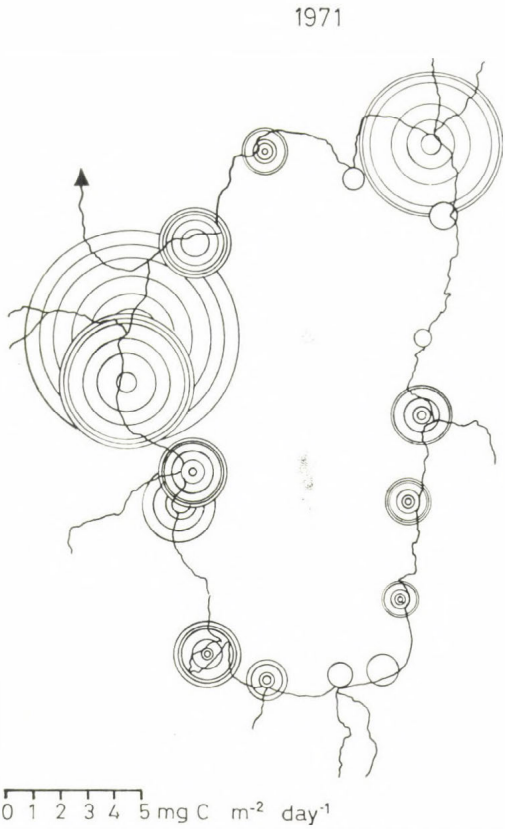


Fig. 6. Periphyton growth per day between 1 May 1971 and 15 July 1971 as measured by organic carbon increase over a 14 day period. Glass cylinders were suspended in the lake at a depth of 5 m and changed every 14-days. The increment of the circle radius indicates the average growth per day for the 14-day period. The centre of the circle indicates station location

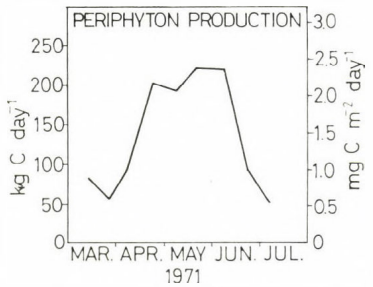


Fig. 7. Periphyton production per day estimates for the entire littoral zone of Lake Tahoe. Calculations are based on the measurement of carbon increase over a 14-day period at each station and the surface area of the station described in the text. The scale on the left indicates the total production for the lake. The scale on the right indicates the average production per square metre for the lake obtained by dividing the total production value by the total surface area of the littoral zone

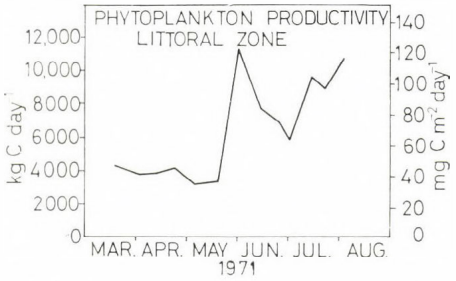


Fig. 8. Phytoplankton productivity per day estimate for the littoral zone of Lake Tahoe. Calculations are based on primary productivity measurements ($^{14}C$ method) at 12 depths at the index station, the productivity of the littoral zone relative to this index station, and the volume of each of 12 layers of water in the littoral zone (from 0 to 100 m)

Phytoplankton productivity for the entire littoral zone of Lake Tahoe was based on *in situ* $^{14}C$ measurements made regularly at 12 depths between 0 and 100 m at our index station near Tahoe Pines (see Fig. 1). The phytoplankton productivity of the littoral zone relative to this index station was estimated from 13 synoptic measurements of primary productivity. Three synoptic surveys were done in 1968 and have been reported by Goldman et al. (1972); four were done in 1969, five in 1970, and one in 1971. They consisted of sampling 32 stations at several depths during a single night and incubating the samples *in situ* during the following light period. Eight of these station locations are pelagic, the others are littoral, and one is our regular index station. The average primary productivity for all 13 synoptics was calculated for all littoral stations to give one littoral value of mgC $m^{-2}$ and for all pelagic stations to give one pelagic value of mgC $m^{-2}$. The phytoplankton productivity of this littoral zone relative to the index station was calculated as a percentage of the average productivity of all littoral stations to the index station. The phytoplankton productivity in the pelagic zone relative to the index station was also calculated as a percentage. These estimated percentages were used to compute the average primary productivity of the phytoplankton on any day in the 12 layers of water in which the littoral zone had been divided corresponding to each depth of the index station. The sum of the phytoplankton productivity of the 12 layers of water was estimated to be the total phytoplankton productivity in the littoral zone that day. Results from these computations made for the period of time that corresponds to our periphyton production study are shown in Fig. 8. The bimodal phytoplankton productivity curve peaked out in early June with the second peak occurring in August. This

was in contrast to the periphyton biomass production curve (Fig. 7), which showed a single high plateau lasting for over two months between April and June.

To compare the total primary production per day of the littoral zone of Lake Tahoe to that of the pelagic zone, the total biomass production per day of the periphyton (Fig. 7) was added to the total phytoplankton productivity in the littoral zone (Fig. 8). The biomass increments of periphyton growth and the rate measures of phytoplankton productivity are not strictly comparable. Combining them, however, should provide a good approxi-

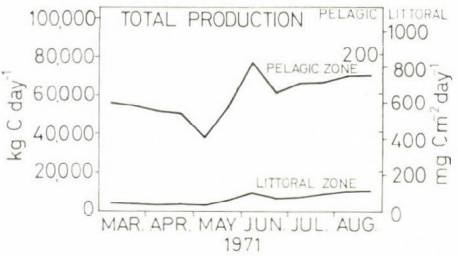


Fig. 9. Total primary production per day of the littoral zone of Lake Tahoe compared to the total productivity of the pelagic zone of the lake. The littoral zone production represents the sum of the biomass production of the periphyton (Fig. 7) and the productivity of the phytoplankton (Fig. 8) for the zone. Calculations of the total primary production per day of the pelagic zone of the lake are based on $^{14}C$ measures of the primary productivity of the index station, the productivity of the pelagic zone relative to the index station, and the volume of water in the euphotic zone of the pelagic region

mation of total littoral production. This was done by planimetering the areas of two-week periods under each curve (Figs 7, 8), computing the corresponding mean value of carbon per day for each community, and adding up these values. The primary productivity per day of the pelagic zone of the lake was computed by correcting the mean productivity per cubic metre at the index station by the percentage that the pelagic zone productivity represents and multiplying by the volume of water in the euphotic zone (0 to 100 m) of the pelagic zone. Results are shown in Fig. 9.

We shall use the term primary production whenever we are referring to either biomass increments only or both biomass increments and $^{14}C$ measurements combined. We shall continue to use the term primary productivity when referring to $^{14}C$ measurements only.

By comparing the primary production curve of the littoral zone of Lake Tahoe with the pelagic productivity curve, we get a graphic impression of the relatively small littoral area involved as well as its contribution to the overall productivity of the lake. Only about 10 per cent of the lake's production is accounted for by the combined phytoplankton productivity and periphyton production down to 100 m. Because of Lake Tahoe's morphometry, the pelagic zone contributes an order of magnitude more carbon to the lake in productivity than does the littoral zone.

Primary productivity in the littoral zone was measured in 1968 with a series of transects. Computer contouring was utilized to display variation in productivity offshore (Goldman and Armstrong 1969). An average of four transects was used to construct each of the vertical profiles of phytoplankton shown in Fig. 10. The Upper Truckee River, which provides 40 per cent of Lake Tahoe's surface inflow, has a highly productive phytoplankton population per unit volume near shore decreasing steadily towards

the pelagic zone. This decrease in productivity per unit volume with depth is inverse to the productivity per unit of surface area. The same is true for the Incline Creek transect except that the fertility of this partially enclosed area (Crystal Bay) is more uniform and probably reflects the less significant volumes of fertilizing inflows. General Creek has been used in our work as a control (Goldman et al. 1972) and the stream influence disappears within a short distance from shore. The transect at Cave Rock, along the sparsely

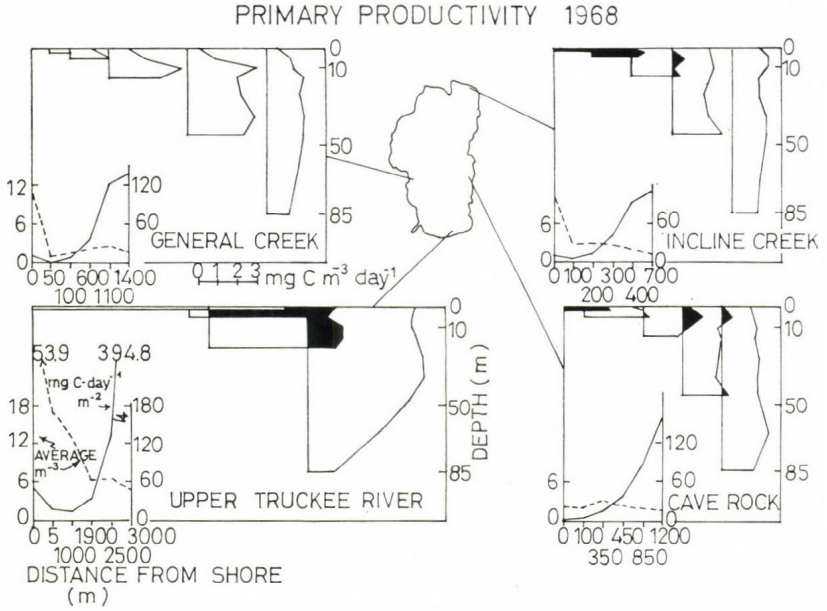


Fig. 10. Phytoplankton primary productivity versus depth at various distances offshore in the littoral zone. Each rectangle represents a different location around the shore of Lake Tahoe. Each point represents an average of four measurements taken on four different days between April and July 1968. The graph inserted on the bottom left of each rectangle shows the variation of the total amount of carbon fixed by the phytoplankton under a square metre of water and the average amount per cubic metre as a function of the distance from shore

settled east shore, shows very little variation in fertility with depth. The steady rise in productivity per unit of surface area simply reflects the steady increase in the photic zone with increasing depth offshore.

## DISCUSSION

The littoral zone of Lake Tahoe is characterized by narrow extent and a relatively small contribution to the overall algal productivity of the lake. Still, it remains the most visible feature of the lake to the largely landbound population and presented the first visible evidence that eutrophication was occurring in the inshore areas. Further, the food chain contribution of the littoral zones of deep lakes like Tahoe and Baikal in the USSR may be much greater than these measures indicate. The luxuriant growths of

periphyton may reflect a restriction of nutrient-enriched waters to the shallow zone of Lake Tahoe by a thermal bar. The periphyton seems particularly sensitive to the spring inflow of nutrients, warming temperature, and increasing photoperiods. The most luxuriant growths of attached algae are usually to be found in the vicinity of stream mouths, but most of the lake's inshore areas are visibly green in spring and early summer. Occasionally, large mats of decaying periphyton and associated bacteria break off and float to the surface or are carried in from streams. Their decay is suspect of triggering a secondary bloom of phytoplankton such as the large lens of *Scenedesmus* that is usually observed near the mouth of the upper Truckee River in spring.

The diversity of the periphyton is similar throughout the year, although the species making up the summer and winter populations are quite different. The lower diversity occurring to the east of the Upper Truckee river mouth is accompanied by a high phytoplankton production. If one accepts the theory that more eutrophic situations are less diverse, this is a logical expectation.

The Truckee River sediment plume extends well along the south-east corner of the lake and appears to reduce periphyton growth through shading or be dissipated and deflected east before it can fertilize the southern stations. It does, however, greatly influence the phytoplankton and planktonic bacteria which thrive in the vicinity of the plume (Goldman et al. 1974).

Because glass substrata are utilized, it seems likely that our estimates of periphyton growth somewhat underestimate natural growth. An irregular substratum provides not only easier attachment, but a variable protection for periphyton growth. The heavy mats that break loose from the wave zone following a spring storm are never duplicated on our slides. Further, we have no real estimate of grazing by the variety of organisms that utilize periphyton as food.

Although aquatic insect larvae and protozoans may graze the periphyton community in Lake Tahoe, the California crayfish *Pacifastacus leniusculus* is probably the most important benthic organism in Lake Tahoe. Studies have shown a distribution of the *P. leniusculus* population between 0 and 60 m depth in Lake Tahoe with maximum densities occurring between 10 and 20 m (Abrahamsson and Goldman 1970). This area of concentration is exclusively in the littoral zone of the lake and may, because of its great abundance, have considerable influence on the ecology of the littoral zone.

Studies on juvenile stages in a number of Decapoda indicate that these animals are strictly algal and detrital feeders (Blegvad 1914). *Pacifastacus* is an omnivore and, in addition to consuming plant and animal food, ingests a variety of detritus and probably a number of benthic organisms including immature aquatic insects (Moshiri and Goldman 1969).

Immature periphyton communities in the littoral zone of Lake Tahoe display a high rate of productivity. As the community develops and the density of growth reaches a maximum, an equilibrium may exist before the winter decline. The mature periphyton community without grazing only produces new cells to replace old and dead cells. The productivity may therefore decrease in a climax or equilibrium state.

It seems likely that the aquatic periphyton community is similar to a terrestrial grassland community which maintains a higher productivity

when they are grazed by herbivores. The presence of a crayfish population in the littoral zone of the lake may increase the productivity of periphyton by grazing pressure and may provide an efficient recycling of nutrients for both attached and free-floating communities which would otherwise be restricted to the periphyton community.

The possibility that the periphyton community is maintained in a more productive state by the grazing of the Lake Tahoe crayfish population seems consistent with the observations in the lake. The primary productivity of Lake Tahoe is very high off Tahoe City. The standing crop of crayfish is also most dense in this area of the lake which may reflect a combination of food supply and abundant cover (Abrahamsson and Goldman 1970).

The shallow water environment of the littoral zone of even a deep lake such as Tahoe is of great interest to the limnologist. Although the water may remain relatively clear it contains higher levels of nutrients than the pelagic waters and has much greater contact with the substrata. The organisms which frequent this zone have the first opportunity to concentrate the nutrients into organic matter. This tends to reduce the amount immediately available for a spring phytoplankton bloom and in a sense buffers the system against loss of transparency. A better understanding of stream and littoral zone periphyton productivity should help to improve our understanding of the dynamics of shallow and deep lakes alike.

*

*Acknowledgements.* This research is currently supported by a Grant-in-Aid from the National Science Foundation's Research Applied to National Needs (RANN) programme (GI-22) and was supported in 1968–71 by E.P.A. Grant 16010 DBU. Special thanks for phytoplankton and periphyton identification and enumeration are due to A. Sands and R. Thomson. Field assistance including SCUBA was under the direction of R. Richards with the assistance of P. Moeller, and M. Perkins. D. Bertrand and Uy Loi Ly assisted in data reduction and M. Smith typed the manuscript.

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# TROPHITÄTSVERHÄLTNISSE IN DEN STAUSEEN DES WESTLICHEN MECSEKGEBIRGES (UNGARN, TRANSDANUBIEN)

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## EINLEITUNG

Das Mecsekgebirge liegt im Donau-Drau-Winkel und erstreckt sich in SW–NO-Richtung in einer Länge von etwa 45 km. Es ist ein Mittelgebirge mit Gipfelhöhen von 600–680 m. Am Südhang des Gebirges liegt die Stadt Pécs (Fünfkirchen), an den Nordhang lehnt sich eine Hügellandschaft an, die aus Löß aufgebaut ist.

Der westliche Teil des Gebirges besteht aus einer domartigen, aus permischem Rotsandstein bestehenden Antiklinale, die im NW von mesozooischen Gesteinen, vornehmlich von Muschelkalk, umsäumt ist (Pálfy 1930). Die Bäche dieses nordwestlichen Gebirgsteils entspringen teilweise aus einigen wasserreichen Karstquellen, teilweise aus kleineren Quellen und entwässern das Gebiet in einem zunächst nach N, dann nach W verlaufenden Talsystem. In diesem Talsystem wurden zwischen 1963 und 1972 vier Stauseen errichtet, die Erholungs- und Sportzwecken dienen. Die Errichtung von zwei weiteren Stauseen soll in der nächsten Zukunft erfolgen.

Von den erwähnten vier Stauseen wurden die limnologischen Verhältnisse der folgenden drei Seen untersucht:

1. Der kleinste der untersuchten Stauseen, der Stausee »Orfűi-tó«, wurde im Jahre 1963 errichtet, ist 9,7 ha groß und besitzt ein Fassungsvermögen von 140 000 $m^3$. Die durchschnittliche Tiefe ist hier weniger als 2 m.

2. Vom ersten Stausee wird das Wasser dem zweiten Stausee »Pécsi-tó« zugeleitet, dem bedeutendsten Glied dieser Stauseenkette, der 80 ha groß ist und ein Fassungsvermögen von 2 700 000 $m^3$ besitzt, mit einer durchschnittlichen Tiefe von 3 m, doch gibt es in diesem See — in der Nähe des Staudammes — auch Wassertiefen um 10 m.

3. Den eigentlichen Erholungszwecken dienen diese beiden Seen, das dritte Glied dieser Kette, nämlich der Stausee »Herman Ottó-tó« (benannt nach dem ungarischen Naturforscher Herman Ottó), soll zu einem Fischreservat bzw. Naturschutzgebiet umgestaltet werden. Dieser See ist 30 ha groß, hat aber wegen seiner geringen Wassertiefe (ca. 1 m) nur 290 000 $m^3$ Fassungsvermögen.

Das vierte Glied dieser Stauseenkette, der Stausee »Kovácsszénájai-tó«, wurde erst im Jahre 1972 errichtet. In diesem See wurden bisher nur einige sondierende Untersuchungen gemacht.

Wir beschränken uns im folgenden auf jene Untersuchungen, die wir an den ersten drei Seen ausgeführt haben. Wie den Angaben zu entnehmen ist, handelt es sich um ausgesprochen seichte Stillgewässer.

Die wasserchemisch-limnologische Bearbeitung dieser Seen begann mit

den Untersuchungen, die in dem Laboratorium für Wassergütekontrolle zu Pécs von Kovács und Vörös ausgeführt wurden. Seit 1972 knüpft sich an diese Arbeit die Tätigkeit von Uherkovich, des Mitarbeiters des Hydrobiologischen Laboratoriums der Akademischen Zentrale zu Pécs an.

Über die physikalisch-chemischen und biologischen Verhältnisse von Stauseen liegen zahlreiche Untersuchungen vor (s. die zitierten Werke von Beger 1966, Uherkovich 1968), doch wurden diese Untersuchungen fast ausschließlich an tiefen, vertikal geschichteten Stauseen ausgeführt und nur verhältnismäßig wenig Daten wurden bisher über seichte Stauseen publiziert (vgl. Uherkovich 1959, 1971).

Zunächst noch eine kurze terminologische Bemerkung: Streng genommen müßte man—angesichts der überwiegend geringen Wassertiefen—im Falle der von uns untersuchten Stauseen eigentlich eher von »Stauteichen« sprechen, doch hat sich dieser Name in der Limnologie noch nicht eingebürgert und so verwenden wir in unseren Ausführungen die Bezeichnung »Stausee«.

Die durchschnittliche jährliche Niederschlagsmenge liegt im Einzugsgebiet der untersuchten Stauseen um 750 mm. Die Verteilung dieser an und für sich beträchtlichen Niederschlagsmenge ist ziemlich ungünstig, in der regenarmen Sommerperiode ist die Verdunstung größer als die Wasserzufuhr durch die speisenden Bäche, und so ist eine regelmäßig zurückkehrende sommerliche Senkung des Wasserniveaus unter den gegenwärtigen stautechnischen Gegebenheiten unvermeidlich.

Die Stauseen sind größtenteils von Ackerland, Wiesen und Weiden umgeben und nur an wenigen Stellen — etwa an 1/8 der gesamten Uferlänge — ist der Ufersaum bewaldet. Das Stauwasser hat bei der Errichtung der Stauseen ebenfalls größtenteils Äcker und Wiesen überschwemmt, mit Ausnahme des dritten Stausees, des »Herman Ottó-tó«, wo nämlich ziemlich große Baumbestände und Hecken überschwemmt worden sind. Auf diese Fragen kommen wir später noch zurück. Es sei erwähnt, daß im Ufersaum der Stauseen eine Aufforstung begonnen hat. Eine umfassende Geländeregulierung und die Anlegung eines Kanalisationsnetzes ist erst in der nächsten Zukunft vorgesehen.

## WASSERCHEMIE UND TROPHITÄTSVERHÄLTNISSE

Die Untersuchungen sollten das allgemeine wasserchemisch-limnologische Bild dieser Gewässer erfassen, unter besonderer Berücksichtigung der gegenwärtigen und in der Zukunft zu erwartenden Gestaltung der Wassergüte. In methodischer Hinsicht dienten vor allem folgende Arbeiten als Grundlage: Felföldy 1972, Szebellédy (Ed.) 1970.

Auf Grund der vorherrschenden Anionen und Kationen ist das Wasser der Stauseen vom Kalzium–Magnesium–Hydrokarbonat-Limnotyp, was dem Ionentyp des Wassers im Einzugsgebiet entspricht. Der Gesamtsalzgehalt der Stauseen liegt um 250–350 mg/l, es handelt sich also um alfa-oligohalobische Gewässer. Die Angaben über den Salzgehalt der einzelnen Stauseen sind in den Sterndiagrammen nach Maucha veranschaulicht (Abb. 1).

Die Trophitätsverhältnisse wurden aus zwei Richtungen untersucht: Einerseits wurden die Stickstoff- und Phosphormengen bestimmt, die im

Wasser für die pflanzliche Produktion vorrätig waren. Andererseits wurde durch die quantitative Chlorophyllbestimmung die Biomasse des Phytoplanktons ermittelt und gleichzeitig über die Gesamtmengen des Bakterioplanktons, des Phyto- und Zooplanktons durch eine Serie von

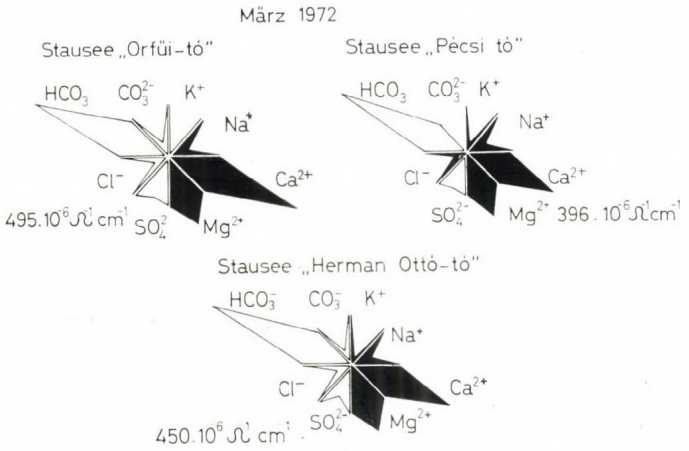


Abb. 1. Anionen-Kationen-Diagramme der untersuchten Stauseen (März 1972)

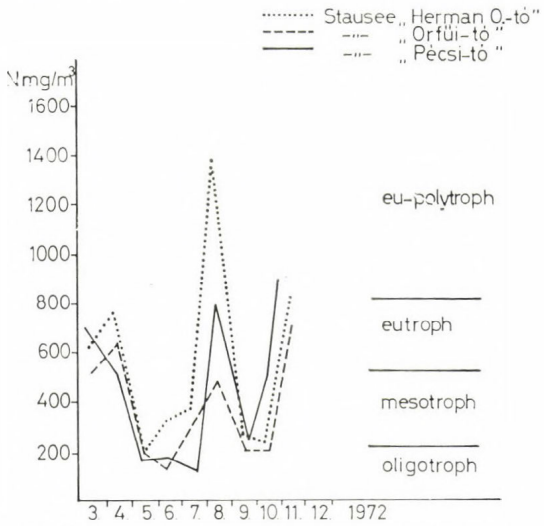


Abb. 2. Änderungen des Stickstoffgehalts im Jahre 1972

mittels Kaliumpermanganatmethode gewonnenen Werten vom Sauerstoffverbrauch Aufklärung erhalten.

Betrachtet man von den Trophitätsparametern die Änderungen des mineralischen Stickstoffgehaltes näher (Abb. 2), erkennt man, daß in den untersuchten Seen ein Stickstoffvorrat zwar stets vorhanden ist, doch ändert sich dieser recht stark im Verlauf der Jahreszeiten. Aus den Kurven geht hervor, daß der Stickstoffvorrat des Stausees »Orfűi-tó« gewissermaßen

beschränkt ist. In den Stauseen »Orfűi-tó« und »Pécsi-tó« kommen zeitweise auch auf einen Ultra-Oligo-Typ hinweisende Stickstoffwerte vor. Im Stausee „Herman Ottó-tó« liegen die Minimalwerte des Stickstoffs im oligo-mesotrophen Bereich. Die Maximalwerte des Stickstoffs finden sich in den drei Stauseen im eutroph-eupolytrophen Bereich. Auf Grund dieser Daten ist anzunehmen, daß in diesen Stauseen der Stickstoff zeitweise ein Minimumfaktor sein kann.

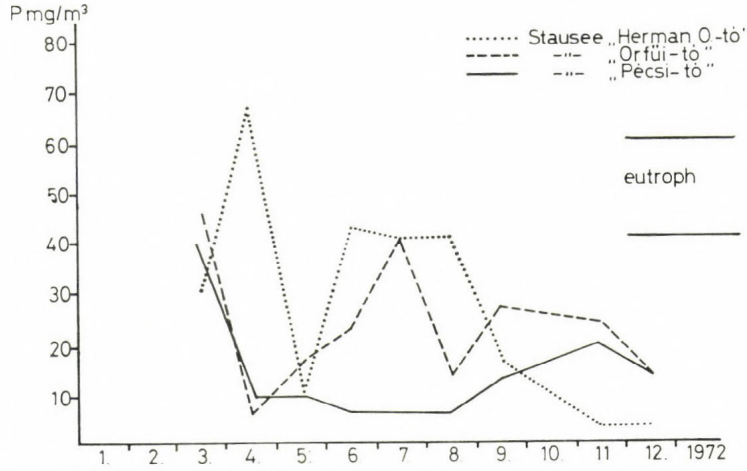


Abb. 3. Änderungen des Gehalts an gelöstem Phosphor im Jahre 1972

Die untersuchten Stauseen lassen sich mit den Gesamtphosphorwerten nicht charakterisieren. Auf Grund dieser Angaben müßte man sie alle dem polytrophen Bereich zuzählen, doch sprechen die übrigen Angaben des Gütebildes dieser Seen gegen diese Annahme. Für das Zustandekommen der hohen Phosphorwerte sind die biologisch unzugänglichen, schwebenden, anorganischen Phosphorverbindungen verantwortlich. (Daß die Bestimmung der Gesamtphorphorwerte im Falle der seichten Stillgewässer unbrauchbar ist, hat sich bereits an anderen Beispielen, z. B. beim Balaton, erwiesen.) Deshalb schien es zweckmäßiger, die untersuchten Gewässer mit den Mengen des gelösten Phosphors zu kennzeichnen.

Die Kurven in Abb. 3 veranschaulichen, daß die Minimalwerte des Phosphors in den untersuchten Seen zum oligo-mesotrophen Bereich gehören, die Maximalwerte dagegen — mit einer einzigen Ausnahme — zum eutrophen Bereich. Angesichts dieser Angaben ist man geneigt anzunehmen, daß in diesen Seen der Phosphor kein limitierender Faktor ist.

Zusammengefaßt: Die Vorräte an Phosphor und Stickstoff ermöglichen eine periodische Zunahme der Eutrophie, was tatsächlich eintritt, u. zw. in den einzelnen Stauseen in unterschiedlicher Weise, da auch das Angebot an Nährstoffen in den einzelnen Seen verschieden ist.

Die Änderungen in der Phytomasse wurden durch die Änderungen des Chlorophyllgehaltes registriert. Es wurden die Gesamtchlorophyllwerte ermittelt, u. zw. mit der Methode von Parsons-Strickland (in: Felföldy 1972). Eine beträchtliche Zunahme des Chlorophyllgehaltes erfolgte in den

Monaten Juni, Juli und August (Abb. 4). In den Stauseen »Orfűi-tó« und »Herman Ottó-tó« führt die Vermehrung des Phytoplanktons bis zur Vegetationsfärbung, was — besonders im Falle des »Orfűi-tó« — eine ungünstige Erscheinung ist. In manchen Fällen entsteht auch im »Pécsi-tó« an den seichten Stellen eine Vegetationsfärbung. (Vgl. dazu die Angaben über das Phytoplankton im nächsten Abschnitt.)

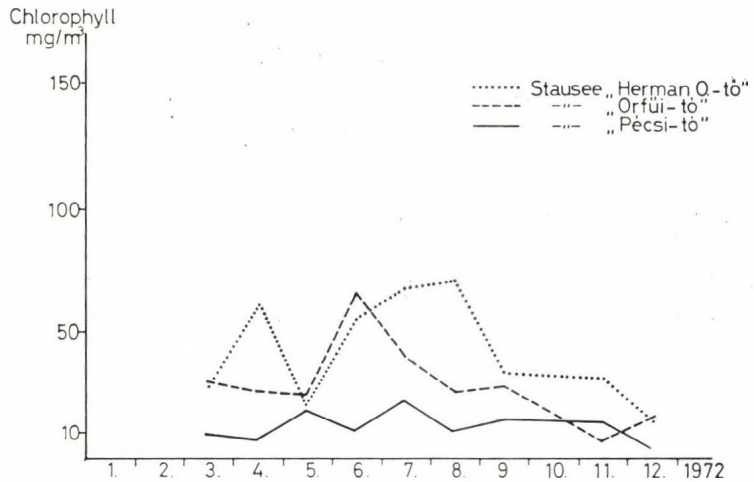


Abb. 4. Änderungen des Chlorophyllgehalts im Jahre 1972

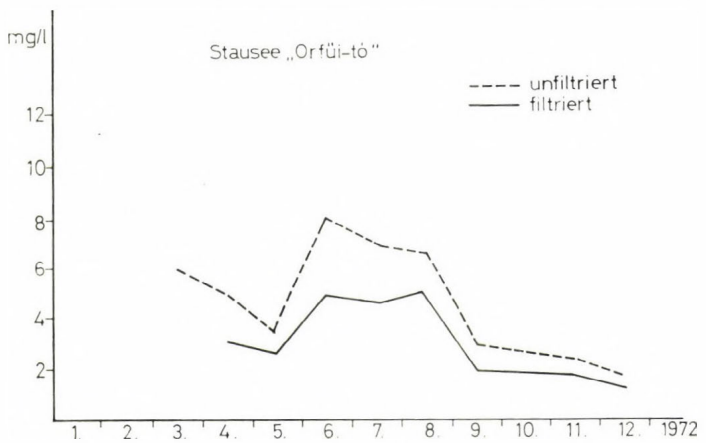


Abb. 5. Sauerstoffverbrauch der filtrierten und unfiltrierten Proben des Stausees »Orfűi-tó« im Jahre 1972

An den Probenentnahmestellen ist eine schwebende organische Verschmutzung allochthoner Herkunft im allgemeinen nicht anzunehmen, folglich ist der mit der Kaliumpermanganatmethode gemessene Sauerstoffverbrauch der filtrierten und unfiltrierten Proben mit der schwebenden Biomasse proportional. Das läßt sich auch an den Kurven der Abb. 5, 6 und 7 veranschaulichen, die vom vorhergehend erwähnten Zusammenhang zeugen.

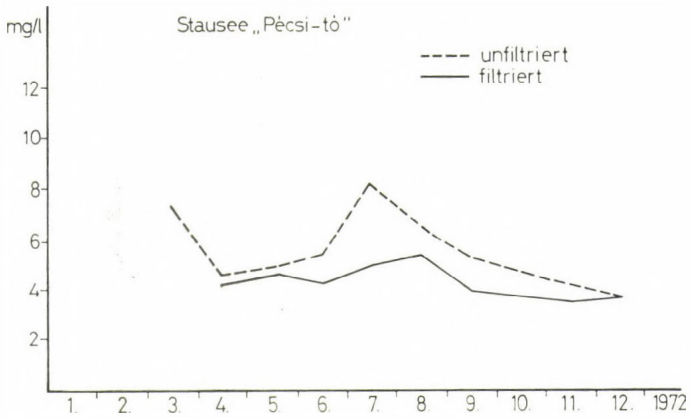


Abb. 6. Sauerstoffverbrauch der filtrierten und unfiltrierten Proben des Stausees »Pécsi-tó« im Jahre 1972

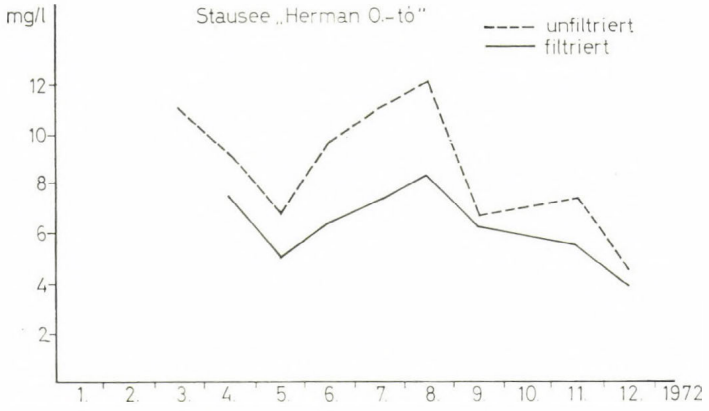


Abb. 7. Sauerstoffverbrauch der filtrierten und unfiltrierten Proben des Stausees »Herman Ottó-tó« im Jahre 1972

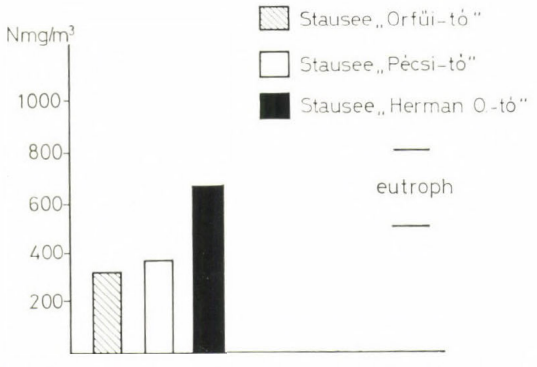


Abb. 8. Stickstoffgehalt der untersuchten Stauseen im Durchschnitt der Sommermonate (Juni–August 1972)

Diese Annahme wird auch durch jenen Umstand bekräftigt, daß die Tendenz der Änderungen im Chlorophyllgehalt weitgehend mit den Änderungen des Sauerstoffverbrauchs übereinstimmt. Der Korrelationskoeffizient (nach Ezekiel-Fox 1970 errechnet) zwischen diesen Werten ist sehr eng, nämlich 0,886; dies beweist eine sehr ausgeprägte Korrelation. Somit ist — nach unserer Auffassung — der mit der Kaliumpermanganatmethode festgestellte Sauerstoffverbrauch in unseren Fällen als Maßstab für die in einem gewissen Zeitraum bestehende Trophität zu verwerten. Es ist freilich in Betracht zu ziehen, daß in solchen seichten Gewässern an verschiedenen Stellen des

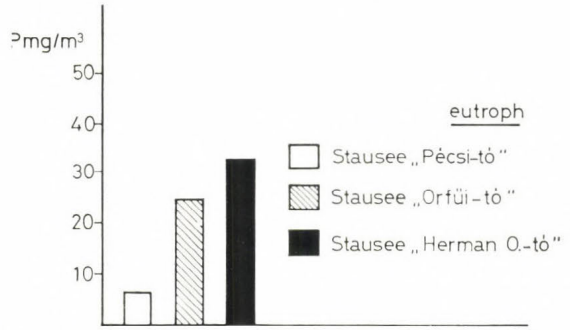


Abb. 9. Phosphorgehalt der untersuchten Stauseen im Durchschnitt der Sommermonate (Juni–August 1972)

Wasserkörpers recht große wasserchemische Unterschiede bestehen, und die Gültigkeit der vorausgehenden Feststellung ist in einem solchen Rahmen zu verstehen.

Auf Grund der untersuchten Trophitätsparameter wurden für die Stauseen verschiedene Reihenfolgen aufgestellt:

1. Nach dem Stickstoffgehalt (Abb. 8).
2. Nach dem Gehalt an gelöstem Phosphor (Abb. 9).
3. Nach dem Chlorophyllgehalt (Abb. 10).
4. Nach dem Sauerstoffverbrauch der Schwebestoffe mit der Kaliumpermanganatmethode gemessen (Abb. 10). (Alle Juni–August 1972.)

Aus dieser zusammenfassenden Aufzählung ergibt sich, daß eine für Erholungszwecke geeignete Wasserqualität allein in den tieferen Stellen der Stauseen »Orfűi-tó« und »Pécsi-tó« zu erwarten und festzustellen ist. An den seichteren Stellen beider Stauseen entfaltet sich dagegen zeitweise ein ausgeprägter eutropher Zustand. Der Stausee »Herman Ottó-tó« ist als ein ständig eutrophes Gewässer zu betrachten.

## PHYTOPLANKTON UND TROPHITÄTSVERHÄLTNISSE

Als Ergänzung zu den dargelegten limnologischen Daten läßt sich folgendes über die quantitative und qualitative Zusammensetzung des Phytoplanktons der betreffenden Gewässer sagen.

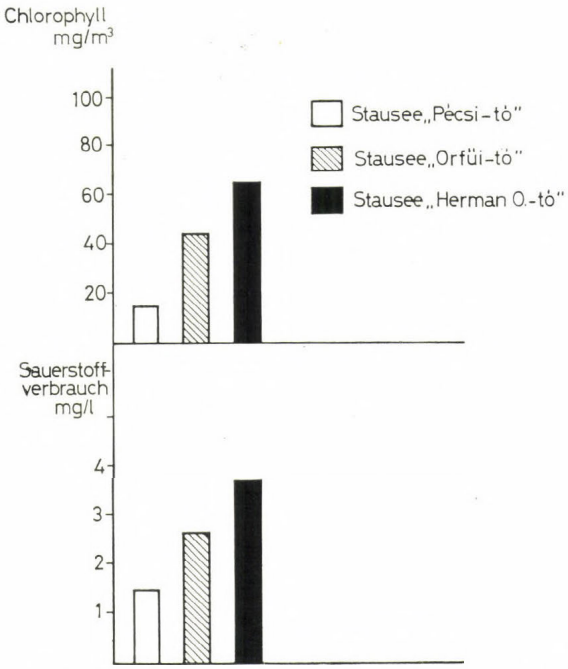


Abb. 10. Chlorophyllgehalt und Sauerstoffverbrauch der untersuchten Stauseen im Durchschnitt der Sommermonate (Juni–August 1972)

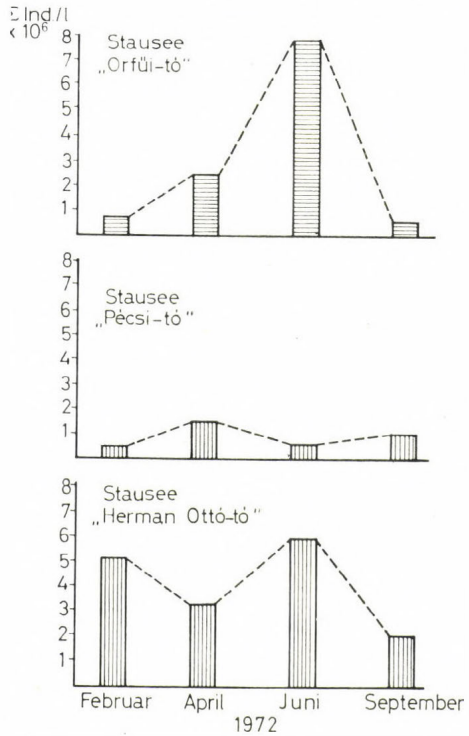


Abb. 11. Jahresverlauf der Gesamtindividuenwerte des Phytoplanktons in den untersuchten Stauseen (1972)

Das Phytoplankton des Stausees »Pécsi-tó« hat unter den drei Stauseen die geringste durchschnittliche Bevölkerungsdichte (Abb. 11). Die maximalen $\Sigma$ Ind./l-Werte blieben in der untersuchten Periode unter 1,5 Millionen, die Minimalwerte lagen um eine halbe Million. Das Bevölkerungsmaximum war das 3,3fache des Minimums. (Vgl. auch Abb. 13.) Nach den quantitativen Phytoplanktonangaben müßte man den Stausee »Pécsi-tó« zu den mesotrophen Gewässern zählen, es kann sich aber bei einer Zunahme der Phosphor- und Stickstoffvorräte (Zuschwemmung von Kunstdünger, Zufuhr von Abwässern usw.) offenbar sehr leicht zu einem ausgesprochen eutrophen Wasser umwandeln.

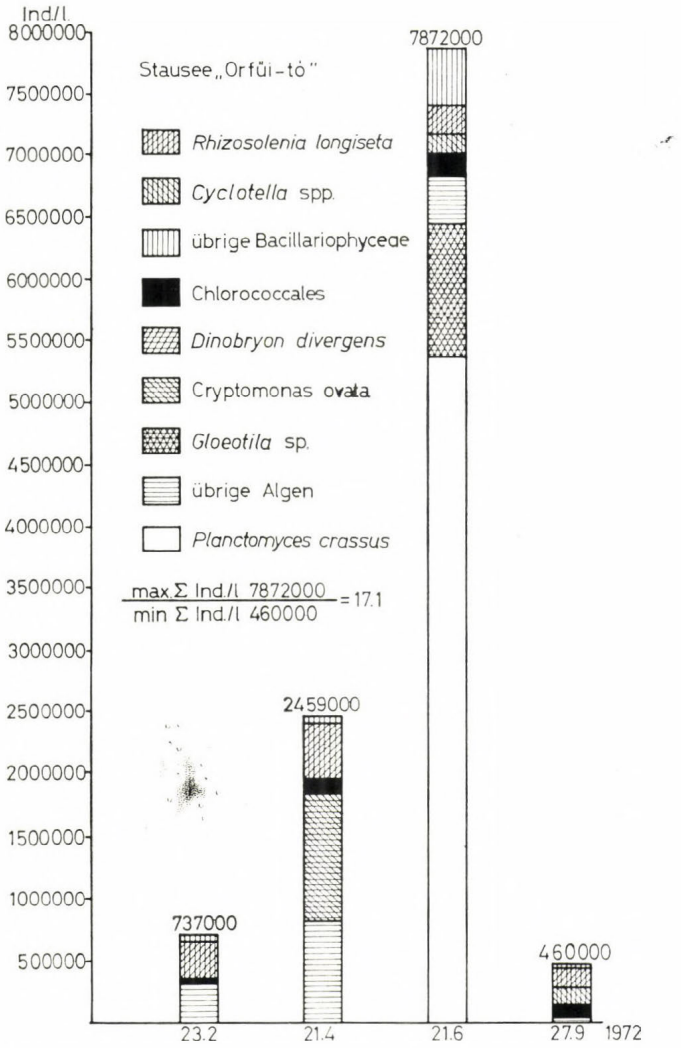


Abb. 12. Hauptzüge der quantitativen Zusammensetzung des Phytoplanktons im Stausee »Orfűi-tó« (1972)

Die $\Sigma$ Ind./l-Werte des Phytoplanktons vom Stausee »Orfűi-tó« schwankten zwischen 460 000 und 7 900 000, das Maximum hat also das Minimum um das 17fache überboten. Dieser See ist der Typ eines von Zeit zu Zeit stark eutrophierten Stillgewässers. Es ist gar nicht vorteilhaft, daß gerade ein solches Wasser das erste Glied der an und für sich labilen Stauseenkette ist (Abb. 11, 12).

Die $\Sigma$ Ind./l-Werte des Phytoplanktons vom Stausee »Herman Ottó-tó« lagen durchschnittlich sehr hoch, um 4 Millionen. Der Maximalwert von 5 900 000 übertraf den Minimalwert von 2 Millionen um das 2,9fache. Dieser Stausee repräsentiert ein Gewässer von ständig hoher Trophität, ist ein echtes eutrophes Wasser mit mehreren polytrophen Zügen (s. Abb. 11, 14).

Die limnologische Individualität der drei Stauseen wird durch die Abweichungen in der qualitativen Zusammensetzung und in den Dominanzverhältnissen ihres Phytoplanktons noch betonter unterstrichen.

Für den Stausee »Orfűi-tó« ist ein ständig hoher *Rhizosolenia longiseta*-Anteil des Phytoplanktons kennzeichnend. Die Produktionsmaxima wurden

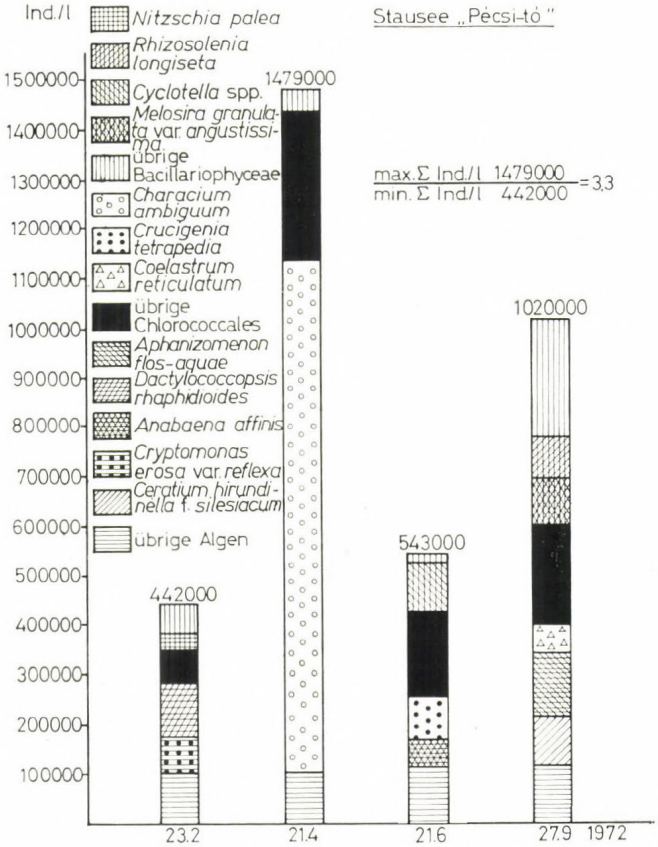


Abb. 13. Hauptzüge der quantitativen Zusammensetzung des Phytoplanktons im Stausee »Pécsi-tó« (1972)

vorwiegend von zwei Mikrophyten, von *Planctomyces crassus* und *Cryptomonas ovata* gebildet (s. Abb. 12).

In dem Stausee »Pécsi-tó« erreicht *Rhizosolenia longiseta* höhere Individuenwerte nur in der Herbstperiode; sonst sind in der Zusammensetzung des Phytoplanktons mengenmäßig einige Chlorococcales-Arten, ferner Blaualgen (so im Frühjahr *Dactylococcopsis rhaphidioides*, im Sommer *Anabaena affinis*, im Herbst *Aphanizomenon flos-aquae*), weiterhin im Frühjahr noch einige *Characium*-Arten von Bedeutung. *Ceratium hirundinella* kommt unter den drei Stauseen nur hier in einer größeren Individuenzahl vor, u. zw. im Frühherbst (Abb. 13).

Die Dominanzverhältnisse im Phytoplankton des Stausees »Herman Ottó-tó« sind grundverschieden von denen der beiden anderen Stauseen. Gegen Ende Winter entfaltet sich hier eine eigenartige *Uroglena volvox*-Dominanz, im Frühjahr wird diese durch die gemeinsame Dominanz von *Cyclotella*-Arten und *Trachelomonas volvocina* abgelöst. Im Sommer ist neben einer aus Ungarn bisher nicht bekannten *Aphanizomenon issatschenkoi*-Dominanz die Subdominanz von *Planctomyces bekefii* und *Planctomyces crassus* auffallend (Abb. 14). (Eine ausführliche Taxonomie der in diesen

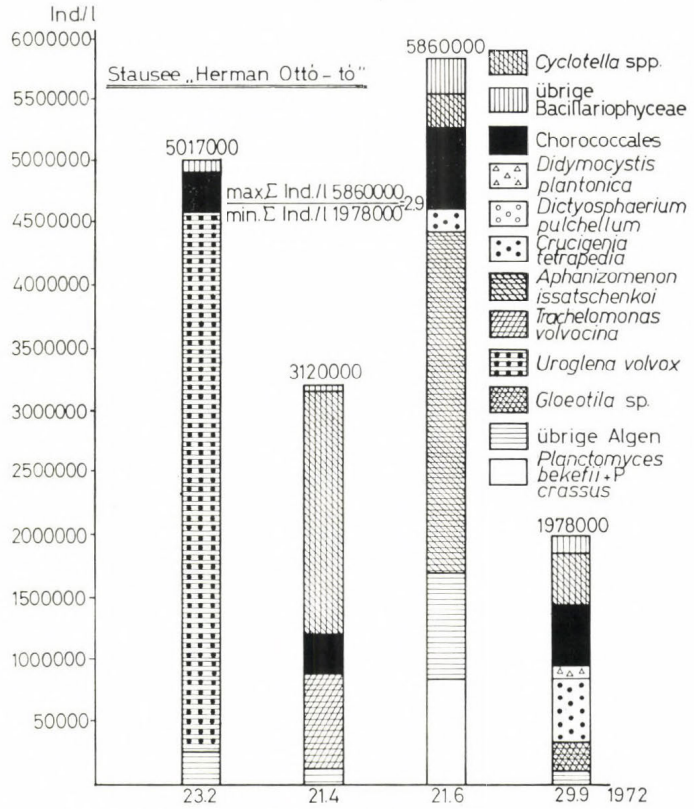


Abb. 14. Hauptzüge der quantitativen Zusammensetzung des Phytoplanktons im Stausee »Herman Ottó-tó« (1972)

Stauseen vorgefundenen Algen soll demnächst in einer besonderen Arbeit veröffentlicht werden.)

Nach den bisherigen Beobachtungen kann man in den folgenden Jahren mit einer gewissen Wiederholung der aufgezählten Dominanzverhältnisse rechnen, doch können sich diese — eben infolge der Labilität dieser seichten Gewässer — auch gewissermaßen umformen, zeitlich umlagern. Die weiteren Beobachtungen werden wohl diesbezüglich endgültigere Aufschlüsse liefern, die sowohl für die praktische Kenntnis dieser Gewässer als auch für eine allgemeinere limnologische Deutung ähnlicher Gewässer von Nutzen sein dürften.

Anschließend sei kurz über eine eigenartige Form der Algenmassenvermehrung gesprochen, die sich im Stausee »Pécsi-tó« im Frühjahr regelmäßig wiederholt. Diese Massenproduktion wurde im März 1973 eingehend untersucht. Es handelt sich dabei in der ersten Phase um eine sog. »Unterwasserbodenblüte«, bei welcher Blaualgen, vornehmlich *Oscillatoria limosa*, an seichten Stellen des Sees am Boden zusammenhängende Algenteppiche bilden. Diese erheben sich dann an die Wasseroberfläche und bilden dort an dieser sekundären Stelle eine Wasserblüte, die in dem untersuchten konkreten Fall etwa 1/5 der gesamten Wasserfläche des Stausees bedeckte. Bei windiger Wetterlage werden diese Algenmatten ans Ufer getrieben, wo dann ihre Verwesung einsetzt. Am 23. 3. 1973 hat eine solche — aus einer Bodenblüte ausgegangene — Wasserblüte eine 16 ha große Fläche des »Pécsi-tó« eingenommen. Diese Wasserblüte hat nach unseren Analysen 676 kg Chlorophyll enthalten; auf Grund dieser Angabe repräsentierte die Wasserblüte 22,6 Tonnen organischer Kohle. Solche und ähnliche Algenmassenvermehrungen sind für die eutrophen Stillgewässer der gemäßigten Zone bekannt und charakteristisch.

## BESPRECHUNG DER WICHTIGSTEN ERGEBNISSE

Versucht man die Ursachen der unterschiedlichen Trophitätsverhältnisse der drei untersuchten Stauseen zu erklären, so ist vor allem folgendes zu bemerken:

Die Trophitätsverhältnisse des Stausees »Orfűi-tó« sind deshalb so unausgeglichen, weil dieser verhältnismäßig kleine Stausee von Verschmutzungen zeitweise stärker belastet wird.

Das verhältnismäßig niedrigere Trophitätsniveau des Stausees »Pécsi-tó« läßt sich auf die größere Wassermenge, die größeren Wassertiefen, ferner auf einen spärlicheren Makrophytenbestand am Ufer zurückführen.

Das ausgeglichen hohe Trophitätsniveau des Stausees »Herman Ottó-tó« hat seine Ursachen in dem durch die Überschwemmung ins Wasser geratenen reichen organischen Material, ferner in den Zerfallprodukten, die aus den zwei weiter oben liegenden Stauseen dahin geleitet werden und wahrscheinlich auch in den höheren Wassertemperaturen in der Vegetationsperiode. In dieser Stauseenkette kommt nämlich das überleitete Wasser in das nächste Glied immer aus der obersten, wärmsten Wasserschicht und so wird die Wassertemperatur der Stauseenkette entlang allmählich höher. An einem Augusttag 1972 wurde z. B. im »Orfűi-tó« 26 °C, im »Pécsi-tó«

schon 28,8 °C und schließlich im »Herman Ottó-tó« 31 °C Wassertemperatur gemessen.

Die Angaben, die über die zeitweise in großer Individuenzahl auftretenden Algen ermittelt wurden, können manches zur Beurteilung des Indikationswertes dieser Algen für eine zunehmende Eutrophierung beitragen. (Vgl. die Problemstellungen der Arbeiten: Felföldy 1970, Uherkovich 1970/71.)

Die Forschungen, die an diesen und ähnlichen Stauseen in den nächsten Jahren noch fortgeführt werden sollen, dienen sowohl allgemeinen limnologischen als auch praktischen Zielen. Sie verfolgen unter anderem das Ziel, auf limnologischer Grundlage eine gewisse Vorhersage über die künftig in Aussicht stehende Wassergüte zu ermöglichen. Die teilweise rein theoretischen Ergebnisse sind auch für die Praxis, für die Planung an diesen Stauseen gewissermaßen Warnzeichen und wir möchten hoffen, daß diese Warnzeichen von der Praxis rechtzeitig und richtig verstanden und verwendet werden.

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*Symp. Biol. Hung.*, *15*, pp. 77–95 (1975)

# COMPARISON OF PELAGIAL AND LITTORAL PRIMARY PRODUCTION IN A SOUTH BOHEMIAN FISHPOND (CZECHOSLOVAKIA)

by

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## INTRODUCTION

The present study is a contribution to the Czechoslovak IBP/PT-PP Section (Productivity of Wetland Biome), the field studies of which were completed in 1972. The stands in the Opatovický pond were studied from the point of view of production by a team headed by D. Dykyjová from 1964. In 1972 during the vegetation period and, as far as possible, during the whole year the primary production of microphytes, the qualitative composition of algal populations and the amount of chlorophyll in algae in the selected pure stands of emergent plants were determined in order to obtain the percentual ratio of microphytes in the total primary production of the stands. Preliminary conclusions are given in a report by Komárková (1973).

The Opatovický pond belongs to the fishpond system of the Třeboň basin. The maximally flooded area is 160.55 ha with 24.3 ha (= 15 per cent) of littoral vegetation. The maximum depth is 3.3 m, the average depth of the pelagial zone being 1.8 m. In 1972, the pond was stocked with 30.9 tons of two-year-old carp and in the same year a natural production of 0.21 tons per ha was achieved. This approximates the average production of the previous years.

Exclusively inorganic fertilizers with a small amount of mineralized soil compost were used to increase carp production. In 1972, the fertilization consisted of lime (24.0 tons), limestone (17.5 tons), superphosphate (3.0 tons), and potassium salts (20.8 tons).

## STANDS AND STATIONS

In the course of the amelioration of the pond, particularly the water level was measured and most of the littoral stands became flooded throughout the year. The stations were situated in a littoral of this type. The station in the pelagial zone was selected in about the centre of the main water body. Figure 1 and Table 1 include more detailed characteristics of the stations and the stands.

## METHODS

In order to determine phytoplankton and periphyton primary production, the oxygen light and dark bottles (LDB) technique was applied. LDBs were suspended in pairs at various depths either from a float or from sticks

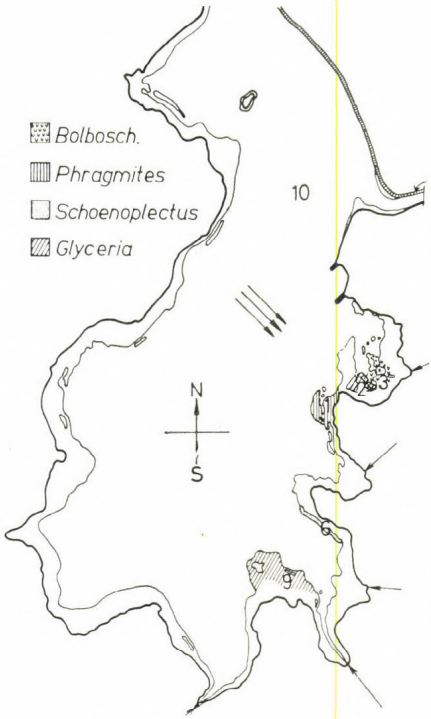


Fig. 1. Situation of the Opatovický fishpond near Třeboň and location of the stations and stands

situated inside the stands. The oxygen determination was carried out by the Winkler method. During the period of dense water-bloom, the method modified by Bruhns was used.

Periphyton production was measured according to Pieczyńska (1965). Whole stalks were cut off close to the bottom and so were leaves, and together with a litter carefully removed from a defined area (5–25 $dm^2$). The whole material was washed, occasionally scraped off into 2–6 l of pond water which had previously been either strained or filtered off depending on the quantity of algae. After that, the animals were removed and the water containing the periphyton was siphoned into light and dark bottles. At the same time the production of the washing water was measured.

Always two parallel samples were exposed *in situ* below the surface and at the depth where the last periphyton had been found. The exposure, even in the case of phytoplankton, lasted only a part of the day (2–4 h), usually about noon. A whole-day exposure was found to be too long for the studied type of water. The full-day production was calculated by using the coefficient of the day exposure irradiation (data of the Kipp and Zonen solarimeter type CM 1).

Algal biomass for determining chlorophyll was concentrated on Millipore filters of a pore size of 0.5 $\mu$m (produced by Synpor VCHZ Synthesia, Czechoslovakia). After that the samples were mechanically ground together with a small amount of magnesium carbonate and pulverized carborundum (300 mesh). Since nitrocellulose filters were used we could not employ Lorenzen's method (1967).

The standard deviation of the sampling and of the primary production and chlorophyll content of periphyton in the stands of *Phragmites* and *Schoenoplectus* was calculated. Thirty random samples—each of a 5 $dm^2$ area—were taken from over stands of 50 $m^2$. The periphytic cover on the stalks was about 25 cm. The stalks and the rest of the leaves were washed into 2 l of filtered pond water. The results are expressed in units per $dm^2$ of the water surface.

The values of primary production were obtained after a 3-hour parallel exposure of LDBs in a depth of 30 cm below the water surface inside the stand to ensure the same light conditions for all samples. The values of

TABLE 1

*Main characteristics of the littoral stations studied*

| No. of location | Distance from open water (m) | Stand | Area of stand (ha) | Density of stalks/m²* | Height of emergent plants (m) | Annual production (dry wt/m² of max. stand, crop)* (g) | Note |
|---|---|---|---|---|---|---|---|
| 1 | 20 | *Phragmites communis* | 0.74 | 61 | 2–2.5 | 872 | = 'locality V' in Hejný (Ed.) (1973) |
| 2 | 6 | *Glyceria maxima*<br>*Utricularia neglecta* | 0.50 | 202 | 0.5 | 970<br>6.9 | floating stand<br>—<br>temporary inflow from pig farm |
| 3 | 10 | *Bolboschoenus maritimus* | 0.60 | 72 | 0.6 | 334 | |
| 6 | 3 | *Schoenoplectus lacustris* | 0.15 | 157 | 1.3 | 650 | narrow belt of ±5 m width |
| 9 | 50 | *Glyceria maxima*<br>*Utricularia neglecta* | 1.0 | 189 | 0.4 | 659<br>2.5 | in limosal ecophase |

* Average data of previous years.

standard deviation in the primary production and chlorophyll content (Table 2) were different concerning *Phragmites* and *Schoenoplectus*, possibly due to the species composition of the periphyton. It can be seen that the density of the periphytic cover greatly varied. This must be taken into consideration in using any method for determining the primary production of periphyton.

The drawback of the LDB method modified for periphyton is that by separating the periphyton from the substrate, the algae lose their original microclimate so that the studied communities assimilate under planktonic rather than periphytic conditions. Owing to this, the method of Assman (1951) is recommended (IBP Handbook, No. 12), according to which whole stalks of plants (*Equisetum*) are exposed in Liebig's light and dark condensers. This method was applied on stems of *Schoenoplectus lacustris* (Table 3). Several parallels of the stems were exposed *in situ* in the condensers, filled with the same filtered water. The periphyton was washed and scraped off from the stalks and the chlorophyll content determined. It was confirmed that both the periphyton and the tissue of the substrate assimilate if the periphyton is thin or covers only a part of the stalk. It is impossible to determine the production by the stalks if the oxygen method is used. By scraping off the periphyton the shading effect of periphytic organisms is

TABLE 2

*Statistical data for estimating the production and chlorophyll content of periphyton ($n = 30$)*

| | *Phragmites*, June 15, 1973 | | |
|---|---|---|---|
| | BPP of periphyton | chlorophyll *a* in periphyton | Quality |
| | mg $O_2$/5 dm² (3 h) | µg/5 dm² | |
| $\bar{x}$ | 1.03 | 80.7 | Bacillario-phyceae |
| $s_{\bar{x}}$ | ±0.31 | ±20.4 | |
| coefficient of variation | ±30.5% | ±25.3% | Chlorophyceae |

| | *Schoenoplectus*, August 2, 1973 | | |
|---|---|---|---|
| | BPP of periphyton | chlorophyll *a* in periphyton | Quality |
| | mg $O_2$/5 dm² (3 h) | µg/5 dm² | |
| $\bar{x}$ | 2.70 | 303.3 | *Stigeoclonium farctum* Berhold |
| $s_{\bar{x}}$ | ±0.96 | ±102.3 | |
| coefficient of variation | ±35.5% | ±33.6% | Bacillariophyceae |

eliminated. If dead stalks are used, the output of the photosynthesis is strongly decreased though the chlorophyll concentration from the washed and scraped off stalks can be compared with the other concentrations.

Another problem is the choice of the corresponding stalks and of periphyton for exposure in the light and dark condensers. According to our results, Assman's method has been found to be unsuitable for the stalks, the green parts of which are submerged in water. The method is either painstaking, since only one stalk or one leaf can be exposed in the container to avoid the shading effect, or not precise enough, if several samples are exposed. Wetzel (1965) reports that the oxygen method is not convenient for vascular plants because part of the produced oxygen is retained inside the plant tissues and is, therefore, not available to the chemical process. This error would evidently also impede the method of Assman if used for the estimation of productivity of both stalks and algal periphyton.

Since the method we have used for determining the primary production of periphyton is not included into those recommended by IBP, we wanted to learn more about the error arising from the removal of the periphyton from the substrate. The method of the inactive substrate was checked in two experiments. Both of them were performed in the same way, i.e. the

TABLE 3

*Comparison of the methods of measuring periphyton primary production according to Assman (1951) and Pieczyńska (1965). Averages, ranges are given in brackets*

| | *n* (pairs) | BPP mg $O_2$/h · 100 m² of *Schoenoplectus* surface | chlorophyll *a* µg/100 cm² of periphyton on *Schoenoplectus* surface |
|---|---|---|---|
| Green stalks with periphyton | 16 | 0.69 (0.51–0.99) | 156.1 (118.4–219.0) |
| Green stalks, periphyton removed | 16 | 0.60 (0.40–0.68) | — |
| Dead stalks with periphyton | 14 | 0.41 (0.33–0.48) | 160.2 (99.6–170.0) |
| Removed periphyton in water | 16 | 0.35 (0.24–0.48) | 170.8 (120.5–180.4) |

periphyton in suspension (scraped off) and that in the original substrate of an adequate surface were exposed in the thermoluministat (18 °C and 22 °C, 3000 W) for $2^1/_2$ hours. Wide-necked 250 ml bottles were used and the centrifuged pond-water served as washing-water. One hour prior to the beginning of the experiment, the water was bubbled through with air. After exposure, the content of each bottle was gently shaken and siphoned into two 50-ml oxygen bottles. From the rest of the suspensions and the periphyton the chlorophyll content was estimated.

The first experiment was carried out with spring periphyton growing on old stems of *Phragmites* (April 1973). The periphyton formed an easily removable slime which contained mostly diatoms and young stages of

TABLE 4

*Gross primary production and concentration of chlorophyll a in periphyton growing on dead stems of Phragmites in spring. Averages, ranges are given in brackets*

| | *n* | BPP, mg $O_2$/hour · 50 cm² of the *Phragmites* surface | % | chlorophyll *a* µg/50 cm² of the *Phragmites* surface | % |
|---|---|---|---|---|---|
| Dead stems with periphyton | 18 | 0.40 (0.32–0.51) | 100 | 35.2 (24.0–42.0) | 100 |
| Dead stems, periphyton removed Both exposed | 18 | 0.39 (0.30–0.45) | 97.5 | 34.0 (26.3–39.1) | 96.6 |

TABLE 5

*Gross primary production and concentration of chlorophyll a in periphyton growing on PVC-belts. Averages, ranges are given in brackets*

| Parts of the PVC-belt | *n* | | BPP mg $O_2$/h·40 cm² of the belt | % | chlorophyll *a* µg/40 cm² of the belt | % |
|---|---|---|---|---|---|---|
| Near the level | 14 | on the belt | 0.61 (0.35–0.69) | 100 | 32.2 (22.5–42.0) | 100 |
| | | removed | 0.37 (0.25–0.55) | 60.6 (40–90.6) | 29.5 (29.0–33.6) | 91.6 (80–110) |
| Above the bottom | 14 | on the belt | 0.13 (0.12–0.23) | 100 | 13.9 (11.9–15.0) | 100 |
| | | removed | 0.10 (0.08–0.20) | 73 (57–100) | 12.9 (12.4–18.9) | 92.8 (79–100) |

*Tribonema* and *Microspora*. For the second experiment we used a 15-day-old periphyton grown on dark coloured PVC belts having been suspended in the pond inside the *Schoenoplectus* stand in August. The summer periphyton was distinguished by the dominance of firmly attached colonies of *Stigeoclonium farctum*. Moreover, diatoms were present. The PVC belts were cut into adequate parts, the upper and the lower parts being investigated separately. The lower part of the belt contained a greater number of animals and a small portion of algae.

The results of the above experiments are given in Tables 4 and 5. While in the first case the periphyton could be easily removed, in the second one a scraper had to be used to remove the initial stages of *Stigeoclonium farctum*.

TABLE 6

*Averages and ranges of more important chemical and physical data in*

| | *n* | 10–open water | | 6–*Schoenoplectus* | |
|---|---|---|---|---|---|
| | | $\bar{x}$ | range | $\bar{x}$ | range |
| Temperature, °C | 12 | 13.6 | 3–22 | 14.0 | 3–22 |
| Transparency, m | 12 | 1.3 | 0.4–2.5 | | |
| pH | 12 | 8.2 | 7.6–9.5 | 8.3 | 7.3–8.9 |
| Alkalinity, mEq/l | 10 | 2.0 | 1.2–2.5 | 2.05 | 1.4–2.5 |
| Hardness, °germ. | 3 | 4.8 | | | |
| $O_2$ mg/l | 12 | 9.8 | 8.3–7.9 | 11.7 | 7.2–18.3 |
| $NO_3$–N, mg/l | 9 | 0.09 | 0.02–0.37 | 0.08 | 0.004–0.295 |
| $NO_2$–N, mg/l | 10 | 0.022 | 0.002–0.081 | 0.022 | 0.001–0.057 |
| $NH_3$–N, mg/l | 11 | 0.70 | 0.30–1.54 | 0.70 | 0.38–1.36 |
| Organic-N dissolved, mg/l | 9 | 1.62 | 0.25–3.03 | 2.35 | 0.11–5.60 |
| $PO_4$–P, mg/l | 10 | 0.063 | 0.11–0.23 | 0.11 | 0.007–0.344 |
| Total P dissolved, mg/l | 8 | 0.84 | 0.03–3.10 | 0.22 | 0.016–0.460 |

In the first experiment we found roughly the same production in both groups of parallels, in the second experiment (Table 5), oxygen production of the scraped-off periphyton was about 40 per cent lower than that of the intact ones.

In the first experiment, the chlorophyll content of the periphyton merely washed off from the stems was similar to that obtained by scraping. Part of the removed algal cells was completely destroyed resulting in a loss of chlorophyll. The other part was partly destroyed, with their photosynthetic activity thus decreasing. This corresponds to the difference between the photosynthetic activity and the chloropyll content.

*Stigeoclonium farctum* and other colonies firmly attached to the substrate appeared in the periphyton in our littoral only at the end of the vegetation season when the shading effect of the fully developed stands was the greatest and the production of periphytic algae declined.

The experiments have proved that the oxygen method used, modified by Pieczyńska, is not suitable for uncontrolled losses of the damaged cells during the removal of the periphyton. It seems that none of the methods determining the production from the differences of the oxygen content in the light and dark bottles is suitable, if only the production of periphyton is to be determined. The $^{14}C$-method could also not be used without corrections because of the great amount of bacteria and organic matter in the littoral of our ponds. The other estimations based on biomass, on its nitrogen content or organic matter are impeded by the presence of animals and organic detritus.

At all the stations studied in 1972, the main chemical and physical measurements were made on pH, alkalinity, oxygen content, hardness, $NO_3$—N, $NH_3$—N, organic N dissolved, $PO_4$—P and total P. All the methods used are described in Hrbáček et al. (1962), and detailed data are given in Komárková and Přibil (1973). The averages and ranges for the season studied (March—November 1972) are given in Table 6. For the qualitative composition of phytoplankton and periphyton throughout the year see Komárek (1973*a*, *b*) and Komárek et al. (1973).

*March–November, 1972 in the Opatovický fishpond*

| 1–*Phragmites* | | 3–*Bolboschoenus* | | 9–*Glyceria* | |
|---|---|---|---|---|---|
| $\bar{x}$ | range | $\bar{x}$ | range | $\bar{x}$ | range |
| 13.2 | 3.0–20.5 | 14.1 | 3–22 | 15.8 | 3.0–23.0 |
| 8.21 | 7.4–9.25 | 7.7 | 6.4–9.4 | 7.6 | 5.7–8.6 |
| 2.0 | 1.2–2.6 | 2.11 | 1.2–2.6 | 2 | 1.4–2.6 |
| 10.5 | 6.3–13.9 | 8.7 | 5.1–13.2 | 11.4 | 6.3–19.9 |
| 0.04 | 0.001–0.075 | 0.05 | 0.002–0.109 | 0.05 | 0.002–0.129 |
| 0.026 | 0.007–0.078 | 0.027 | 0.004–0.084 | 0.021 | 0.002–0.093 |
| 0.55 | 0.16–0.94 | 0.68 | 0.31–1.33 | 0.51 | 0.28–1.00 |
| 2.92 | 0.25–4.90 | 2.35 | 0.17–4.34 | 2.01 | 0.36–4.36 |
| 0.06 | 0.008–0.176 | 0.10 | 0.01–0.30 | 0.07 | 0.021–0.158 |
| 1.36 | 0.01–8.90 | 0.71 | 0.015–3.30 | 0.06 | 0.013–2.400 |

## RESULTS OF THE SEASONAL STUDY OF PHYTOPLANKTON AND PERIPHYTON IN THE LITTORAL AND THE INFLUENCE OF THE OPEN WATER

The seasonal courses of the main chemical and biological data are shown in Figs 2–7. They are discussed in greater detail in a paper by Komárková (1973).

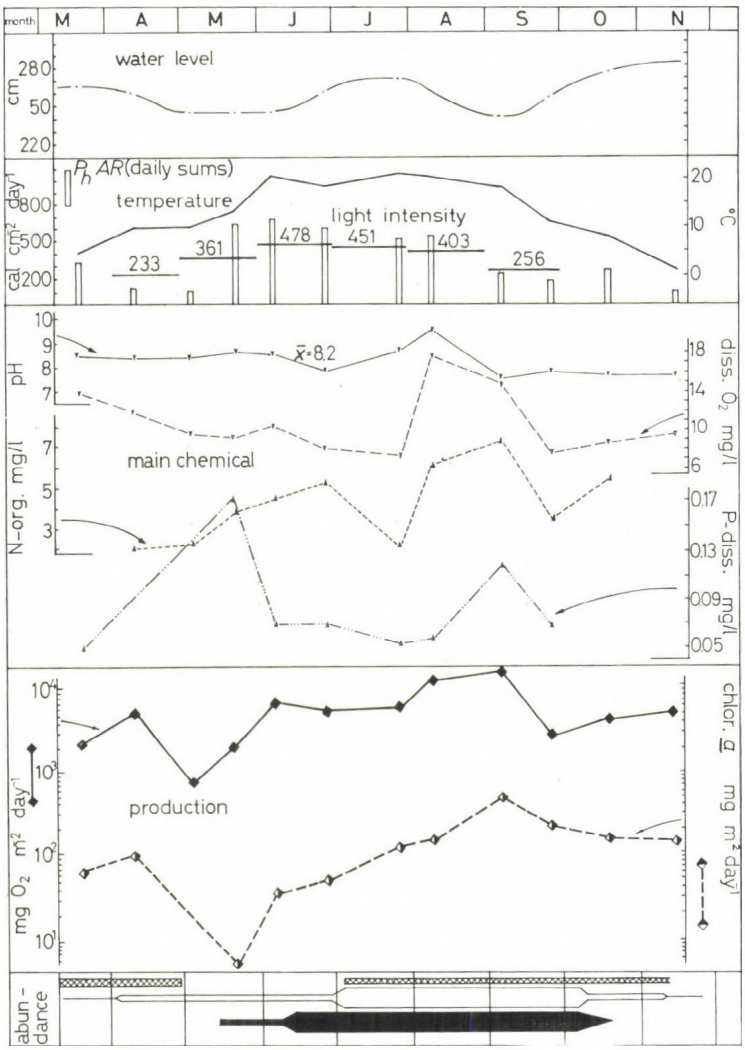


Fig. 2. Course of the 1972 production data of phytoplankton (locality 10) in the Opatovický fishpond compared with the main ecological factors. The light intensities represent monthly means of the daily sums of global radiation and daily sums of $P_hAR$ on the days of measuring. For explanation of the groups of algae see Fig. 7

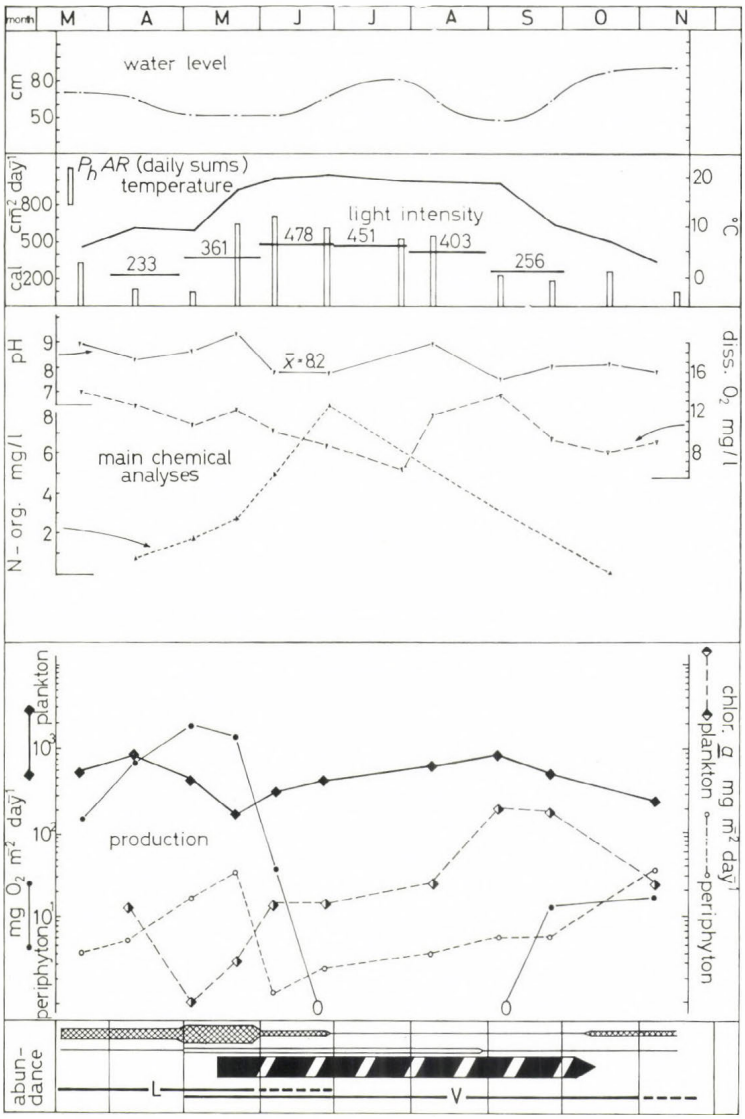


Fig. 3. Course of the 1972 production data of phytoplankton and periphyton in the *Phragmites*-stand (locality 1) in the Opatovický fishpond, compared with the main ecological factors. The light intensities represent monthly means of the daily sums of global radiation and daily sums of $P_hAR$ on the days of measuring. For explanation of the groups of algae see Fig. 7

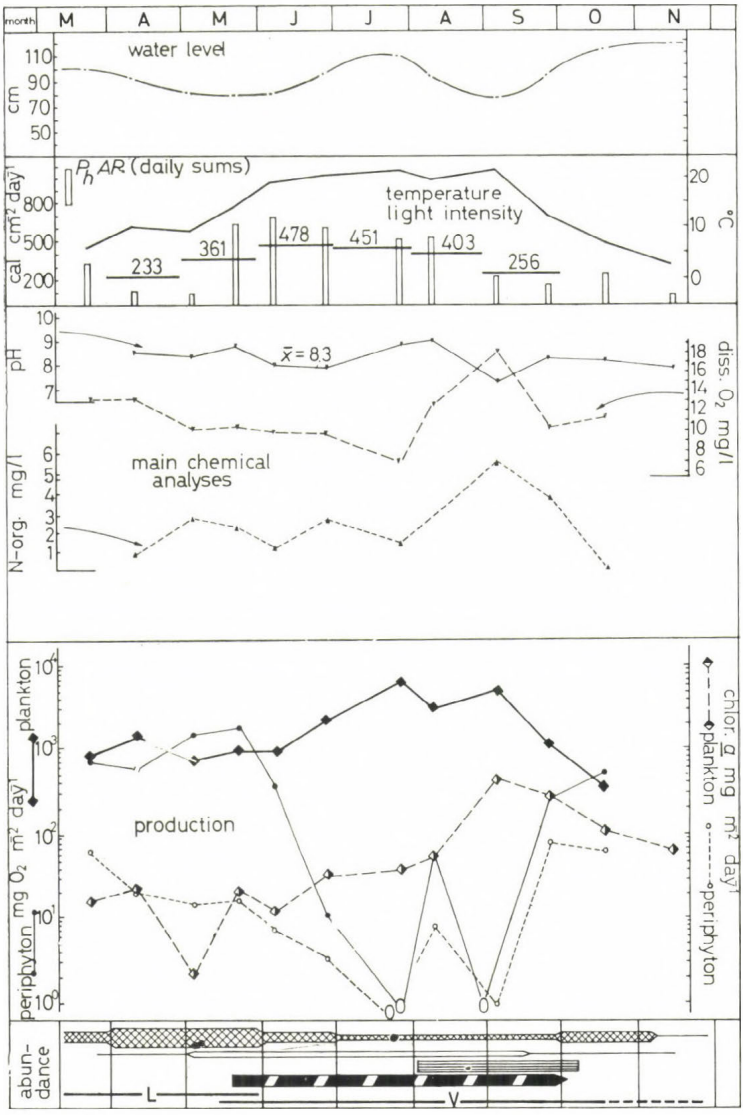


Fig. 4. Course of the 1972 production data of phytoplankton and periphyton in the *Schoenoplectus*-stand (locality 6) in the Opatovický fishpond compared with the main ecological factors. The light intensities represent monthly means of the daily sums of global radiation and daily sums of $P_hAR$ on the days of measuring. For explanation of the groups of algae see Fig. 7

We found a great influence of the chemism of open water on the quality of water inside the littoral stands studied. The chemism of the open water was influenced, to some extent, by fertilization. The effect of the chemism of water (organic N dissolved, oxygen content) was most conspicuous at station No. 9 (*Glyceria*-stand) in spring when a great amount of filamentous

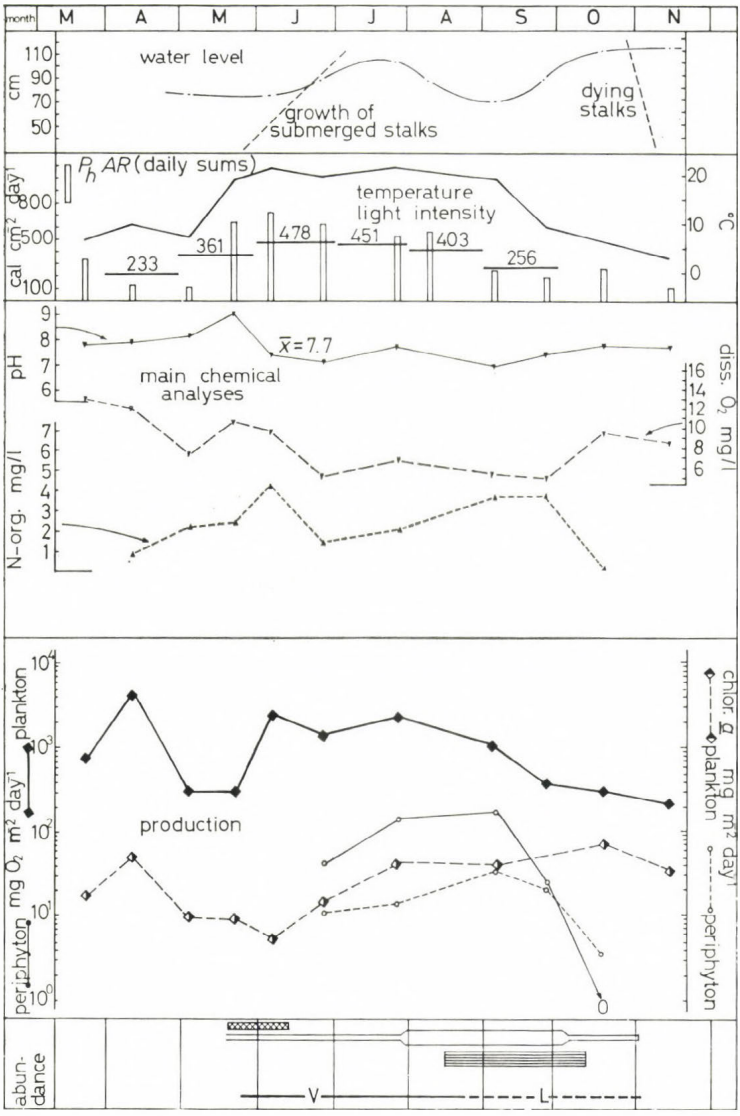


Fig. 5. Course of the 1972 production data of phytoplankton and periphyton in the *Bolboschoenus*-stand (locality 3) in the Opatovický fishpond compared with the main ecological factors. The light intensities represent monthly means of the daily sums of global radiation and daily sums of $P_hAR$ on the days of measuring. For explanation of the groups of algae see Fig. 7

algae appeared followed by a great population of *Daphnia*. Other extreme values appeared inside the stand of *Phragmites* (Fig. 3).

From the point of view of primary production and chlorophyll content, most similar to the pelagial was station No. 6 (*Schoenoplectus*), owing to the character of the stand, i.e. a narrow belt of leafless stalks exposed to wind

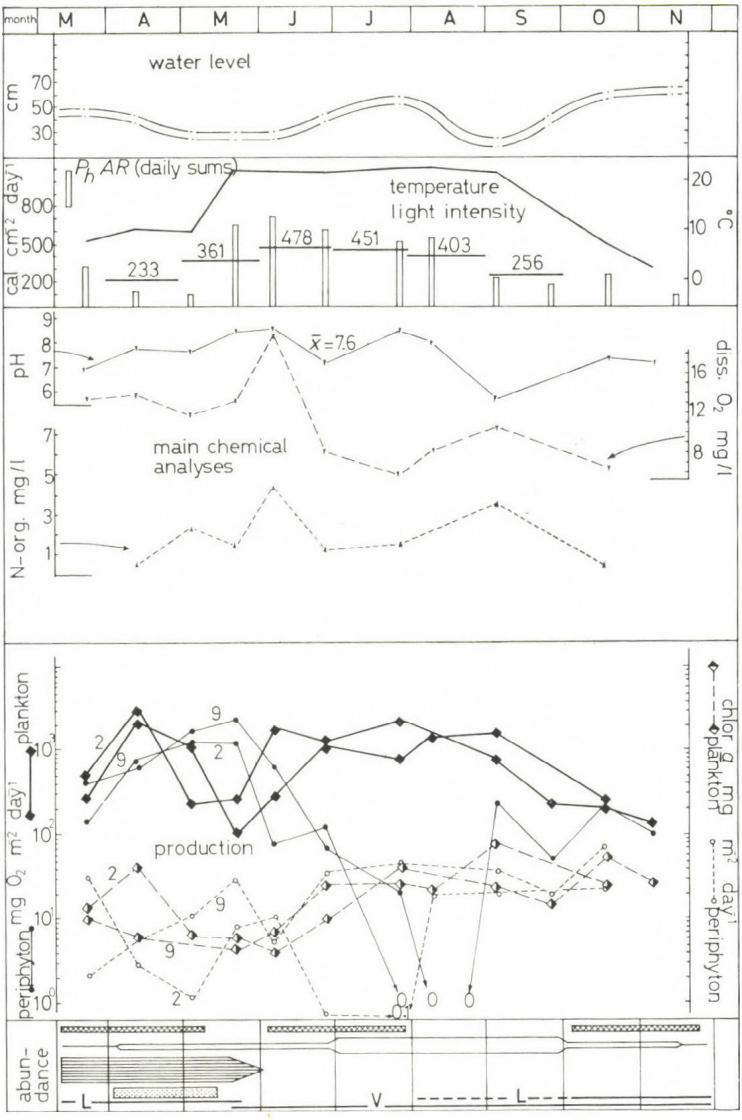


Fig. 6. Course of the 1972 production data of phytoplankton and periphyton in localities 2 and 9 of *Glyceria*-stand, in the Opatovický fishpond compared with the main ecological factors. The light intensities represent monthly means of the daily sums of global radiation and the daily sums of $P_hAR$ on the days of measuring. For explanation of the groups of algae see Fig. 7

action. Somewhat less affected were the stands of *Bolboschoenus* and *Glyceria* (stations No. 9 and No. 2) had the smallest contact with the open water (*Glyceria* in limosal ecophase). A particular case is represented by station No. 1 (*Phragmites*), being strongly influenced by large amounts of cyanophycean water-bloom blown from the pelagial by the prevailing winds

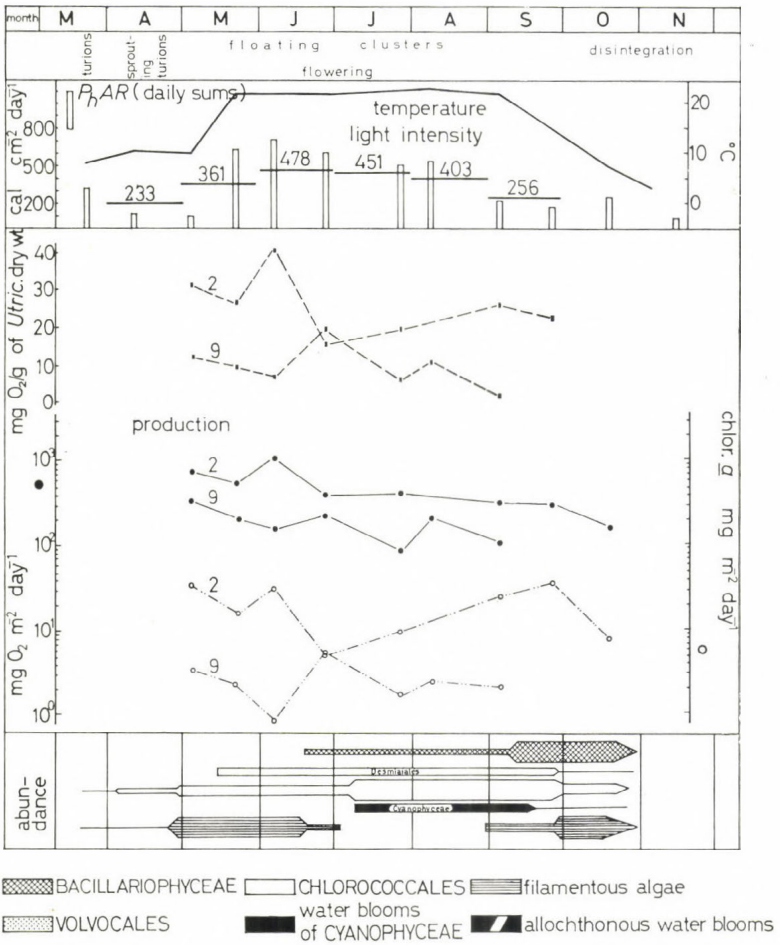


Fig. 7. Course of the 1972 production data of periphyton of floating *Utricularia*-clusters in localities 2 and 9 in the Opatovický fishpond. The light intensities represent monthly means of the daily sums of global radiation and daily sums of $P_hAR$ on the days of measuring

during summer (the amount of chlorophyll see in Fig. 3). Under strongly reduced light conditions the water-bloom decayed, contributing only slightly to the primary production. This was not observed in the other stands because the regular arrangement of the stalks of *Phragmites* allows the water-bloom to penetrate deep into the stands.

There is no specific littoral plankton in the Opatovický fishpond either, concerning the abundance of phytoplankton throughout the year (cf. Straškraba 1963). The abundance of algal species varies according to locality. The similarity of the sets of planktonic species at the studied stations is based (Fig. 8) on the calculation of the homotoneity index (according to Sørensen 1948, Moravec 1971) among the planktonic communities in

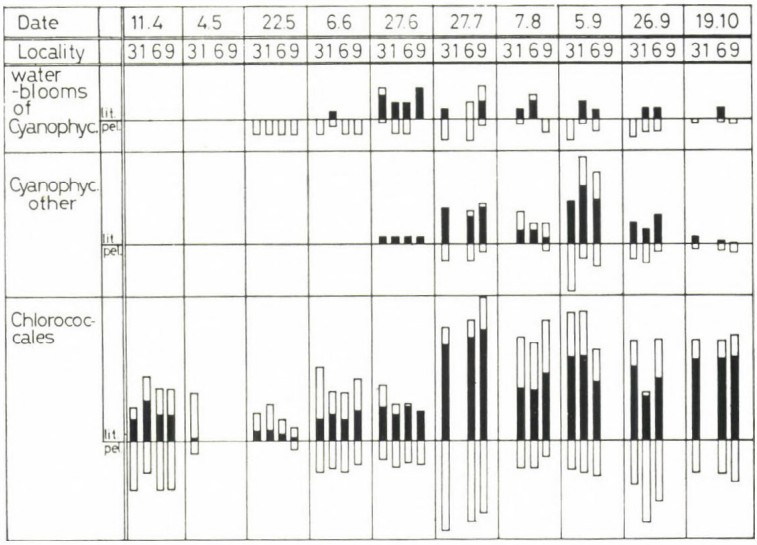


Fig. 8. Interaction between the pelagial and littoral in the species composition of phytoplankton in the studied localities in 1972. The black columns represent the percentage of species occurring in both biotopes, the white columns the species occurring only in the littoral (lit.) or pelagial (pel.). Localities: 3 = *Bolboschoenus*, 1 = *Phragmites*, 6 = *Schoenoplectus*, 9 = *Glyceria*

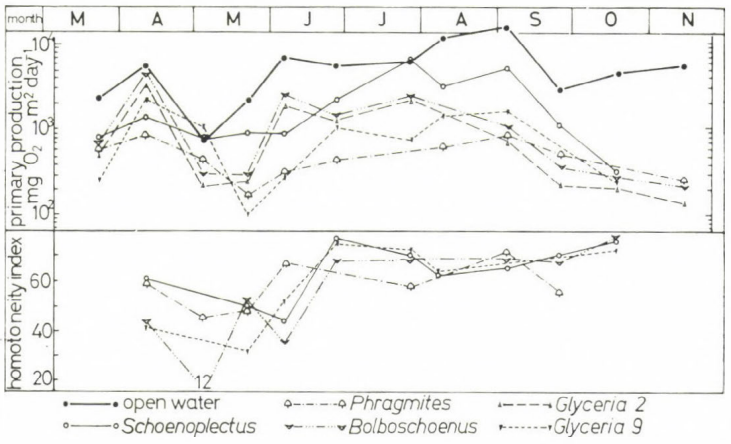


Fig. 9. Comparison of plankton primary production (mg $O_2$ $m^{-2}$ $day^{-1}$) in the open water and in different littoral stands and the course of homotoneity index (calculated according to SØRENSEN 1948) of the phytoplanktonic communities (open water: different littoral stands) in 1972

the littoral and pelagial (Fig. 9). The homotoneity index was similar at all stations, especially during summer ranging between relatively high values (60–70 per cent). It is noteworthy that the greatest differences in the species composition of the littoral and pelagial phytoplankton production were observed in spring when the stands of littoral plants are relatively low and thin.

The differences in the qualitative composition of periphyton of the individual stands were thoroughly studied by Komárek et al. (1973). A series of species specific for periphyton was defined but no substantial differences were found in the composition of periphyton between the individual stations. A specific and characteristic composition of algal populations was observed only in periphyton growing in the clusters of *Utricularia*.

## ANNUAL PRODUCTION OF MICRO- AND MACROPHYTES IN THE OPATOVICKÝ POND

We calculated the total (March–November 1972) production of microphytes taking into account the course of daily solar radiation during the days of sampling and also all other days. Table 7 contains the measured values. In order to compare the production of individual components of the total primary production in the stands, all data were transferred to annual net production and expressed in kcal per $m^2$ (Table 8). The data on macrophytes are the average values of the maximal above-ground biomass for homogeneous stands estimated by Dykyjová and Ondok (personal communi-

TABLE 7

*Seasonal production of micro- and macrophytes (actually measured data)*

| Microphyte, gross primary production in g $O_2/m^2$ (season: March–November 1972) | | | | | | |
|---|---|---|---|---|---|---|
| locality | 10–pelagial | 6–*Schoenopl.* | 1–*Phragmit.* | 3–*Bolbosch.* | 2–*Glyceria* | 9–*Glyceria* |
| Phytoplankton | 1,491.6 | 490.9 | 161.6 | 343.1 | 261.3 | 249.9 |
| Periphyton on macrophytes | | 166.8 | 131.5 | 119.6 | 118.4 | 152.0 |
| Periphyton on *Utricularia* | | | | | 64.4 | 23.6 |
| Macrophyte, seasonal max. biomass in g dry wt/$m^2$ (maximal standing crop-averages 1972) | | | | | | |
| Emergent macrophytes (density) | | 650 (157) | 872 (61) | 334 (72) | 970 (202) | 659 (189) |
| *Utricularia* | | | | | 6.9 | 2.5 |

TABLE 8

*Ash content and oxycalorific coefficients (kcal/g org. wt) of the macrophytes studied in stands*

| | *Schoenoplectus* | *Phragmites* | *Glyceria* | *Bolboschoenus* | *Utricularia* |
|---|---|---|---|---|---|
| Per cent of ash | 7.0 | 6.5 | 7.3 | 8.0 | 20 |
| Oxycalorific coefficient kcal/g org.wt | 4.3 | 4.8 | 4.5 | 4.3 | 4.5 |

TABLE 9

*Net production of the different components of littoral vegetation*

| | | 10–open water | | 6–*Schoenoplectus* | | |
|---|---|---|---|---|---|---|
| | | kcal/m² | | kcal/m² | | % |
| | | micro | macro | micro | macro | |
| Phytoplankton | gross | 5,152 | | 1,696 | | |
| | net | 3,864 | | 1,272 | | 29 |
| Periphyton on emergent macrophytes | gross | | | 602 | | |
| | net | | | 451 | | 11 |
| Periphyton on *Utricularia* | gross | | | | | |
| | net | | | | | |
| Microphytes, total | | 3,864 | | 1,732 | | 40 |
| Emergent macrophytes | net | | | | 2,604 | |
| *Utricularia* | net | | | | | |
| Macrophytes, total | | | | | 2,604 | 60 |
| Primary production, total | | 3,864 | | 4,336 | | 100 |

cation). Thus the measured values were transferred to energetic units using the coefficients found for the studied stands (Table 9).

According to Westlake (1965), the net primary production of the stand corresponds to the maximum value of the seasonal standing crop. Exceptions are the stands of *Glyceria* the annual losses of which amount to about 15 per cent. According to the predetermination of Dykyjová, we raised the total above-ground biomass by 10 per cent.

We assumed, furthermore, the production of phytoplankton and periphyton during the winter months to be comparable with the data of Pieczyńska and Szczepańska (1966) in Masurian lakes where the production of phytoplankton was 10.7 per cent and that of periphyton 15.6 per cent of the year's yield for three winter months: December, January and February. The annual production of periphyton did not similarly increase in the stands of *Bolboschoenus maritimus* and *Utricularia neglecta* whose stems are incapable of persisting throughout the winter. Additionally, it must be noted that the production of periphyton is underestimated, to a certain extent, when the results of the above experiments are considered.

As no sufficient data are available on the relationship between the actual production and data measured during our determinations we analysed our data without any corrections. Even if the production of periphyton were raised by about 10 per cent it would share only by a small percentage in the total production of the littoral. Clusters of *Utricularia* in which

*in the 6 localities in the Opatovický fishpond*

| 1–*Phragmites* | | | 3–*Bolboschoenus* | | | 2–*Glyceria* | | | 9–*Glyceria* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| kcal/m² | | % | kcal/m² | | % | kcal/m² | | % | kcal/m² | | % |
| micro | macro | | micro | macro | | micro | macro | | micro | macro | |
| 558 | | | 1,184 | | | 902 | | | 863 | | |
| 418 | | 9 | 888 | | 36 | 676 | | 12 | 647 | | 15 |
| 474 | | | 373 | | | 427 | | | 548 | | |
| 356 | | 7.5 | 279 | | 11 | 320 | | 5.5 | 411 | | 10 |
| | | | | | | 201 | | | 74 | | |
| | | | | | | 151 | | 2.5 | 55 | | 1 |
| 774 | | 16.5 | 1,167 | | 47 | 1,147 | | 20 | 1,113 | | 26 |
| | 3,913 | | | 1,321 | | | 4,450 | | | 3,024 | |
| | | | | | | | 232 | | | 85 | |
| | 3,913 | 83.5 | | 1,321 | 53 | | 4,682 | 80 | | 3,109 | 74 |
| 4,687 | | 100 | 2,488 | | 100 | 5,829 | | 100 | 4,222 | | 100 |

the production of periphyton several times exceeds that of higher plant might be of interest.

The fact that the total production of the littoral zone (including secondary production) is much lower than that of the pelagial one was proved by Straškraba (1963) who studied two ponds with shallow littoral in the Blatná region (South Bohemia) from the viewpoint of fish production during the summer season. His data are based on the nitrogen content of the samples; consequently, it is impossible to differentiate the algal component by itself.

Data on the primary production of the littoral in lakes are given by Pieczyńska and Szczepańska (1966). Although they studied the conditions in a similar type of littoral, using the same method, they found the production of periphyton to be the same as that of phytoplankton. It seems that the littoral zone of a lake and that of a fertilized pond differs in this sense.

The total annual production for individual stands was the highest at station No. 2 (*Glyceria* stand), and next to it, at station No. 9, also a *Glyceria* stand with the highest water level.

From the point of view of primary production, in all our stands macrophytes were the most important and, at the second place, phytoplankton despite that its production was limited by the water level. The periphyton, was least important producing only large amounts of filamentous algae in spring. For great part of the vegetation period the algal production was strongly limited by the shading effect of the macrophyte stands.

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# SCHÄTZUNG DER PRIMÄRPRODUKTION IM TOTEN DONAUARM VON TOLNA UND IM WASSER DES SEES NAGYSZÉKTÓ VON KISTELEK

von

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Mehrere Jahre hindurch wurden in verschiedenen Jahreszeiten die produktionsbiologischen Verhältnisse des toten Donauarmes von Tolna (Dvihally 1971a) sowie einen ganzen Sommer lang wiederholt die biologischen und chemischen Verhältnisse des Sees Nagyszéktó von Kistelek (Dvihally und Ponyi, 1957) untersucht. Die Untersuchungen haben sich auf den Sauerstoffhaushalt, die wasserchemischen Verhältnisse und die optischen Eigenschaften sowie auf die Primärproduktion der beiden stehenden Gewässer erstreckt.

Der wichtigste gemeinsame Zug beider Gewässer ist die im Vergleich zur großen Wassermenge verhältnismäßig geringe Tiefe. Dennoch unterscheiden sie sich voneinander in bezug auf die chemischen Verhältnisse in hohem Grade. Während der tote Donauarm von Tolna in der chemischen Zusammensetzung die chemischen Eigenschaften des Donauwassers bewahrt, also ein Gewässer vom $Ca^{++}-HCO_3^-$-Typ ist, ist der Nagyszéktó von Kistelek eines der charakteristischen $Na^+-CO_3^{--}-HCO_3^-$-haltigen Natrongewässer der Großen Ungarischen Tiefebene (Alföld).

Der tote Donauarm von Tolna hat eine Fläche von 143,84 ha und ist ein durchschnittlich 1–2 m tiefes stehendes Gewässer, dessen Ufer von flachem Waldgelände und landwirtschaftlich bebautem Gebiet umgeben ist. Der Grund des Flußbetts ist mit schwefelwasserstofffreiem schwarzem Schlamm bedeckt. Eine höhere Vegetation oder submerse Wasserflora gibt es hier kaum, doch ist das Wasser reich an Plankton. Der Arm wurde an beiden Seiten mit einem starken Dammsystem vom eigentlichen Strom abgetrennt. Der seit vielen Jahrzehnten selbständige Donauarm kommt selbst bei den größten Überschwemmungen nicht mit dem Strom in Verbindung, das Sediment des Fließgewässers hat sich auf seinem Grund abgelagert, wodurch sich die Durchsichtigkeitsverhältnisse des Wassers im Hinblick auf die Entwicklung des Planktons günstig verändert haben. Auch der Temperatur- und Stoffhaushalt haben sich langsam umgestellt, das Wasser wurde eutropher und die Produktion von organischem Stoff der in ihm entstandenen und für stehende Gewässer typischen Lebensgemeinschaft übertrifft wesentlich die Primärproduktion des Phytoplanktons der Fließgewässer. Das Wasser ist im Winter durchsichtig, in 1 m Tiefe dringt bis zu 16% der auf die Oberfläche fallenden Lichtmenge ein, hingegen wird es im Frühjahr trüb, gelblichgrün und in 1 m Tiefe ist bloß 0,025% des Lichtes der Oberfläche vorhanden. Zu jeder Jahreszeit ist im Wasser die Transmission des gelblichgrünen Lichtes am größten. Die Gesamtmenge des gelösten Salzes des Wassers liegt zwischen 420–680 mg/l,

der pH-Wert wechselte im Laufe der Untersuchungsjahre zwischen 7,7–8,7.

Der Nagyszéktó von Kistelek ist ein sich mehrere Kilometer lang durch Ackerland, Pußten und Weiden mit Szikboden erstreckender, weniger als 1 m tiefer Natronsee. Seinem Ufer entlang findet sich etwa in 20 m Breite ein Schilfgürtel und innerhalb dieser Zone ein ebenfalls etwa 20 m breiter Binsengürtel. Seine wasserchemischen Verhältnisse zeigen im Laufe des Jahres infolge der Temperaturschwankungen, der Respiration und der im Wasser vor sich gehenden intensiven biologischen Prozesse starke Änderungen. Sein Wasser ist im Sommer, so auch in der Untersuchungsperiode, stark konzentriert, es dominieren in ihm Na,- $CO_3$- und $HCO_3$-Ionen, während die Menge der übrigen gelösten Bestandteile, z. B. die des Kalziums, völlig in den Hintergrund tritt. Der gelöste Gesamtsalzgehalt beträgt im Sommer mehr als 3 000 mg/l, sein pH-Wert liegt über 10! Die Farbe des Wassers ist charakteristisch gelblichbraun, in einzelnen Perioden infolge des Ausscheidens des sich in kolloidem Zustand befindlichen $CaCO_3$ milchartig grau. In das Wasser dringen — im Gegensatz zu dem klaren Wasser und dem Wasser des toten Donauarmes von Tolna — die Strahlen von langer Wellenlänge am tiefsten ein, und deshalb bilden über einer bestimmten Tiefe, im Untersuchungssommer in einer 40–60 cm übertreffenden Tiefe, ausschließlich die Strahlen des roten Farbenbereiches das Licht (Dvihally 1958, 1961, 1971b).

In beiden Seen ist ein lebhafter tages- und jahreszeitlicher Sauerstoffdynamismus wahrzunehmen. Die absolute Menge des gelösten Sauerstoffes ist im Winter in beiden Gewässern stark erhöht, hingegen sind die tageszeitlichen Sauerstoffschwankungen im Winter gering. Im Winter sind also die täglichen Sauerstoffkurven flacher, ausgeglichener als im Sommer. Die Sättigungswerte sowie ihre täglichen Schwankungen sind ebenfalls im Sommer größer als im Winter. Die maximale Sättigung betrug im toten Donauarm von Tolna 240%, im Nagyszéktó von Kistelek 186%.

Die sich auf das Ausmaß der Primärproduktion beziehenden Untersuchungen dauerten in jedem Falle 24 Stunden. Um die vom Gesichtspunkt der Produktion aktive Periode, also die im Laufe des Tages vor sich gehende Produktion fortlaufend, ohne Unterbrechung verfolgen zu können, wurde die 24stündige Periode von 4 Uhr früh des ersten Untersuchungstages bis 4 Uhr des nächsten Morgens gerechnet. In den zwei Seen wurde die Intensität der Primärproduktion einerseits mit der von zahlreichen Verfassern angewandten, bereits als klassisch geltenden Hell-Dunkelflaschen-Sauerstoffmethode untersucht. Die Entnahme der Wasserproben geschah mit dem Maucha-Wereschtschaginschen Wasserprobenentnehmer, wobei mit dem durch ein einziges Schöpfen aus derselben Tiefe entnommenen Wasser sowohl die Hell- als auch die Dunkelflaschen gefüllt werden konnten; aus demselben Wasser erfolgte auch die Bestimmung des Ausgangssauerstoffgehaltes sowie die Ermittlung der mit der Produktion zusammenhängenden wichtigsten Faktoren (Temperatur, Trübheit, pH, Alkalinität usw.). Die Dunkel- und Hellflaschen sind mit eingeschliffenen Pfropfen versehene Glasgefäße von etwa 125 ml Volumen. Die Dunkelflasche wurde außerdem zur Zeit der Exposition auch in eine Alufolie eingepackt. Die Flaschen wurden für 24 Stunden in die gleiche Wassertiefe zurückversenkt, aus der die in ihnen enthaltenen Wasserproben stammten. Aus der Differenz des

Anfangssauerstoffgehaltes und des Sauerstoffgehaltes der 24 Stunden lang exponierten Dunkel- und Hellflaschen wurden die tägliche Brutto- und Nettoprimärproduktion sowie die Respiration errechnet.

Das Maß der Primärproduktion wurde in jedem Fall auch mit der Methode von Odum (1956) sowie Odum und Hoskin (1958), mit der Registrierung der aus den im Wasser der Seen vor sich gehenden Sauerstoffveränderungen gewonnenen 24stündigen Sauerstoffkurve geschätzt. An den Untersuchungstagen wurden 2stündlich die Schwankungen des gelösten Sauerstoffgehaltes im Wasser der Seen an Ort und Stelle gemessen. Die Bruttoprimärproduktion und die Respiration wurden auf Grund der im gelösten Sauerstoffgehalt eintretenden Änderungen graphisch bestimmt. Da der Wert der Sauerstoffsättigung im Laufe des Tages in jedem Falle stark veränderlich war, wurde der Sauerstoffwechsel zwischen Wasser und Atmosphäre, d. h. das Maß der Diffusion für jede Stunde des Tages errechnet und mit diesen Werten wurden die Produktionskurven korrigiert.

Sämtliche Sauerstoffbestimmungen wurden mit der ursprünglichen Methode von Winkler sofort an Ort und Stelle durchgeführt.

Im untersuchten Abschnitt des toten Donauarmes von Tolna kann die produktionsbiologische Rolle des Benthos und des Periphytons vernachlässigt werden, da die limnische Lebensgemeinschaft vor allem planktonisch ist. Deshalb dienten als Grundlage für die Schätzung der Primärproduktion vor allem jene Ergebnisse, die mit der Hell-Dunkelflaschenmethode gewonnen wurden. Demgegenüber ist die Lebensgemeinschaft im Nagyszéktó von Kistelek heterogen, an der Produktion sind sowohl das Plankton als auch die Organismen des Benthos und des Periphytons beteiligt, ja selbst die Rolle der höheren Wasservegetation der Uferzonen kann nicht vernachlässigt werden. Hier wurde also das Maß der Primärproduktion mit den im Wasser selbst vor sich gehenden Änderungen der Sauerstoffverhältnisse, d. h. mit der Registrierung der 24stündigen Sauerstoffkurve geschätzt.

Im Wasser des toten Donauarmes von Tolna schwankte an der Wasseroberfläche die Bruttoproduktion zwischen 2–23 g/m³/Tag, auf dem Grund zwischen 0–5 g/m³/Tag, im Nagyszéktó von Kistelek zwischen 72–122 g/m³/Tag, in Sauerstoffwerten ausgedrückt (Tabelle 1).

Die Bruttoproduktion ist eine grundlegende Angabe und bildet eine Ausgangsbasis zu den weiteren Produktionsberechnungen; in unserem Fall drückt sie die Geschwindigkeit der Bildung des neuen organischen Stoffes, d. h., die der Produktion in Sauerstoffwerten aus, jedoch enthält sie auch die durch die binnen 24 Stunden eintretenden Änderungen der Diffusion, der Respiration und der Biomasse im Ökosystem eintretenden Sauerstoffverluste. Für die Konsumenten des limnischen Lebensraumes ist jedoch von ökologischem Gesichtspunkt die effektiv zur Verfügung stehende, verwendbare organische Stoff- bzw. Sauerstoffmenge wichtig, deren Produktionsintensität vom Wert der Nettoprimärproduktion angezeigt wird. Die Werte der Nettoprimärproduktion schwanken an der Wasseroberfläche im toten Donauarm von Tolna zwischen 0–20, auf dem Grund zwischen 0–3 und im Wasser des Nagyszéktó von Kistelek zwischen 4—44 g $O_2$/m³/Tag. Die Respirationswerte betragen an der Oberfläche des toten Donauarmes von Tolna 2–10, auf dem Grund 0–10 und im Nagyszéktó 24–89 g $O_2$/m³/Tag.

Die Werte der Brutto- und Nettoprimärproduktion waren im Wasser

TABELLE 1

| | | | Bruttoprimärproduktion (P) g $O_2/m^3/24$ h | Nettoprimärproduktion g $O_2/m^3/24$ h | Respiration (R) g $O_2/m^3/24$ h | P/R |
|---|---|---|---|---|---|---|
| | | *Donauarm vom Tolna* | | | | |
| 11. VII. | 1968 | Oberfläche | 8,5 | 7,0 | 3,1 | 2,7 |
| 3–4. XII. | 1968 | Oberfläche | 3,1 | 2,2 | 1,9 | 1,6 |
| | | Wassergrund | 3,0 | 2,7 | 0,6 | 5,0 |
| 14–15. V. | 1969 | Oberfläche | 0,1 | 0,0 | 5,1 | 0,02 |
| | | Wassergrund | 2,6 | 0,0 | 10,4 | 0,25 |
| 22–23. VII. | 1969 | Oberfläche | 23,2 | 20,4 | 5,3 | 4,4 |
| | | Wassergrund | 0,2 | 0,0 | 5,1 | 0,04 |
| 20–21. X. | 1969 | Oberfläche | 14,0 | — | — | — |
| | | Wassergrund | 7,0 | — | — | — |
| 13–14. VII. | 1971 | Oberfläche | 17,5 | 11,3 | 12,5 | 1,4 |
| | | Wassergrund | 1,4 | 0,0 | 10,4 | 0,13 |
| 27–28. IX. | 1971 | Oberfläche | 17,4 | 14,6 | 5,7 | 3,0 |
| | | Wassergrund | 4,6 | 0,0 | 4,8 | 0,95 |
| 15–16. XI. | 1971 | Oberfläche | 8,5 | 6,7 | 3,7 | 2,3 |
| | | Wassergrund | 2,7 | 0,0 | 4,0 | 0,7 |
| 24–25. I. | 1972 | Oberfläche | 3,2 | 2,0 | 2,4 | 1,3 |
| | | Wassergrund | 2,4 | 2,4 | 0,0 | — |
| 20–21. III. | 1972 | Oberfläche | 7,9 | 4,9 | 6,1 | 1,3 |
| | | Wassergrund | 4,0 | 0,0 | 6,7 | 0,6 |
| 15–16. V. | 1972 | Oberfläche | 3,6 | 2,9 | 1,5 | 2,4 |
| | | Wassergrund | 0,6 | 0,0 | 1,7 | 0,4 |
| | | *Nagyszéktó von Kistelek* | | | | |
| 4–5. VI. 1955 | | Freies Wasser | 88 | 44 | 24 | 1,8 |
| 11. VII. 1955 | | Freies Wasser | 118 | 26 | 72 | 0,4 |
| | | Binsengraszone | 122 | 13 | 89 | 0,14 |
| | | Schilfzone | 72 | 4 | 48 | 0,08 |

des toten Donauarmes von Tolna im Sommer höher als im Winter und im Frühjahr, das Maximum erreichten sie im Herbst. Im Vergleich zu den Ergebnissen der mit ähnlichen Methoden durchgeführten Produktionsuntersuchungen ist die Produktionsintensität im toten Donauarm anscheinend größer als z. B. die des Mikołajski-Sees in Polen (Spodniewska 1969), des Smyslovské Jesarnoe sowie des Smyslow-Fischteiches in der Tschechoslowakei (Fott 1972). Auf Grund der Extremwerte seiner Produktion entspricht er im großen und ganzen den von Copeland und Dorris (1962), Ganning und Wulff (1970), McConnell (1962), Odum (1957), Odum und Odum (1955), Odum und Hoskin (1958), ferner von Welch (1968) untersuchten zahlreichen süßen und salzigen Gewässern von Europa und Amerika. Die Brutto- und Nettoproduktion des Nagyszéktó von Kistelek hingegen ist im allgemeinen wesentlich höher als die der erwähnten Gewässer; diese Tatsache weist auf den in den Natrongewässern vor sich gehenden allgemein bekannten lebhaften Stoff- und Energieumsatz hin. Die vom Wind, von der Strömung, vom Wellengang und von der Sauerstoffsättigung abhängende Diffusion entspricht im Falle der von uns untersuchten Gewässer

den Diffusionswerten der von den obigen Autoren beschriebenen seichten Seen, Buchten und aufgepeitschten Gewässer.

Zur Schätzung der Produktion ist die Bestimmung des Quotienten aus Bruttoprimärproduktion und Respiration, d. h. des Verhältnisses des Produktionsprozesses zu den Verbrauchsprozessen, das Wichtigste. In den Perioden, wo die Produktion den Verbrauch übertrifft, häufen sich die entstandenen organischen Stoffe an, an anderen Tagen hingegen, wenn die Respiration gesteigert ist, vermag das Wasser die gespeicherte Energie gänzlich zu verlieren. Im Wasser des toten Donauarmes von Tolna dominiert in der Wasserschicht der Oberfläche das ganze Jahr hindurch der Produktionsprozeß, hingegen übertrifft in der Nähe des Wassergrundes im Laufe des ganzen Jahres die Primärproduktion das Maß der Respiration. In dem nur mit schneefreiem Eis bedeckten Wasser sind die Werte der Produktion und Respiration im Winter am geringsten, jedoch hat die limnische Lebensgemeinschaft selbst in dieser Periode an der Oberfläche mehr organische Stoffe produziert als ihr Verbrauch betrug. Im Sommer und vor allem im Herbst sind die Werte des Quotienten aus Produktion und Respiration um das 2- bis 3fache höher als im Winter, und die Spitzenwerte des Quotienten wurden jedes Jahr im Herbst beobachtet. Nach Odum (1956) ist also im Laufe des Jahres der Stoffwechsel der Wasserschicht an der Oberfläche im toten Donauarm von Tolna autotroph, der des Grundwassers hingegen heterotroph. Die Frage, wo sich die Kompensationstiefe von Fall zu Fall befindet, d. h., wie groß die Produktionsschicht und die Dicke der Verbrauchsschicht der ganzen Wassermenge des Sees in den verschiedenen Perioden ist, also ob letzten Endes der Stoffwechsel der ganzen Wassermenge in Anbetracht der Tiefenproduktionsverhältnisse autotroph oder heterotroph ist, kann erst in weiteren Untersuchungen entschieden werden.

Im Nagyszéktó von Kistelek dominierte im Stoffwechsel der limnischen Lebensgemeinschaft unter sehr günstigen meteorologischen Verhältnissen in einem Fall die Produktion. Die Bruttoproduktion und das Verhältnis der Produktion zur Respiration waren auf den freien Wasserflächen des Sees am höchsten. Die größte tageszeitliche Sauerstoffschwankung und die größte Übersättigung sowie der regste Sauerstoffwechsel zwischen Atmosphäre und Wasser konnten ebenfalls im offenen Wasser beobachtet werden. In den von Binsen und Schilf beschatteten Uferteilen des Sees ist der vom Gesichtspunkt der Produktion aktive Tagesabschnitt, also der »Tag«, viel kürzer, deswegen fallen hier die Intensität der Produktion und der Wert des Quotienten aus Produktion und Respiration bedeutend zurück. Die Sauerstoffuntersättigung erreicht ein hohes Maß und die Diffusion erfolgt in einer Richtung, sie vollzieht sich aus der Atmosphäre in das Wasser und ist im Laufe des Tages fast von gleichem Ausmaß. Einige Wochen später erreichten bei einer anderen Gelegenheit bei windigem, regnerischem, stürmischem Wetter und Abnehmen des Lichtklimas und der Temperatur nicht nur in den von der Vegetation bewachsenen Seeteilen sondern auch in den offenen Gewässern die Verbrauchsprozesse das Übergewicht. Die Respiration übertraf im Laufe des ganzen Tages das Maß der Bruttoprimärproduktion, an diesem Tage wurde also der Stoffwechsel des ganzen Sees heterotroph.

Dieses Beispiel mahnt also zur Vorsicht bei den Produktionsschätzungen. Die Tatsache, daß die biogene Dynamik der Produktionsprozesse als Folge

der Umweltseinwirkungen sehr unterschiedlich, ja selbst von entgegengesetzter Richtung sein kann, bedeutet, daß sich die Ergebnisse ausschließlich auf die Untersuchungsperiode beziehen. Man darf auch nicht vergessen, daß sie ihrem Charakter nach jeweils nur Schätzungen sind. Deshalb vermieden wir es, den Produktionswert eines für die Jahreszeit nicht charakteristischen Tages auf eine längere Zeitperiode umzurechnen. Um für die Primärproduktion monatliche, jahreszeitliche oder jährliche Durchschnittswerte gewinnen oder die produzierte Sauerstoffmenge reell auf Kohle, Glukose oder Energie umrechnen zu können, bedarf es noch ausführlicherer und häufigerer Untersuchungsserien.

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*Symp. Biol. Hung.*, *15*, pp. 103–108 (1975)

# EFFECT OF AN EXPERIMENTALLY CHANGED FISH STOCK ON PHYTOPLANKTON STRUCTURE, BIOMASS AND PRODUCTION IN THE POND-TYPE LAKE WARNIAK

by

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Lake Warniak is a natural eutrophic pond-type lake. Its average depth is 1.5 m, maximum depth 3.7 m and the surface is 38.4 ha. The bottom of the lake is soft and has a thick layer of sediment. Practically, the whole lake is covered with aquatic plants. About 12 per cent of the surface is covered with emerged vegetation (mainly *Phragmites communis* Trin.), the remaining part being covered with submerged vegetation with *Ceratophyllum demersum* L. as dominant and *Stratiotes aloides* L., *Elodea canadensis* Rich., various species of *Potamogeton* and *Charales* as highly abundant species (Bernatowicz 1969).

Research on Lake Warniak has been carried out since 1967 at the suggestion of the Inland Fisheries Institute and in co-operation with the research workers of the same Institute as well as with those from the Department of Hydrobiology, Institute of Ecology of the Polish Academy of Sciences and Institute of Zoology, Warsaw University.

The aim of the extensive studies was to find the possibilities of maintaining a higher fish stock than usual, and to learn the effects of an experimentally changed fish stock on the lake biocenosis. During the first 3 years through introduction of carp and bream the benthophagous fish stock had been gradually increasing. As a result, the benthophagous fish stock and its pressure on benthos and fauna associated with aquatic vegetation increased in 1969 more than twice when compared with the situation before the introduction of fish (Kajak and Zawisza 1973). In 1970 and 1971 the lake was practically unstocked (only single specimens of grass carp and silver carp were introduced). In addition, because of the 'winter-kill' in 1970 (Zachwieja 1973), the bulk of fish died out, the fish stock thus becoming very low.

The effect of fish on the lake biocenosis was analysed by comparing chosen communities in the parts accessible and inaccessible to fish, i.e. in enclosures of different size (ranging from smaller than 1 $m^2$ up to the half of the lake).*

* The following papers are in press: 1. Zachwieja, J.: Physical and chemical conditions in lake water. — 2. Zawisza, J. and Ciepielewski, W.: Changes of the autochthonous ichtyofauna due to the introduction of carp (*Cyprinus carpio* L.). — 3. Ciepielewski, W.: Biomass and production of pike (*Esox lucius* L.). — 4. Prejs, A.: Feeding of introduced and autochthonous non-predatory fish. — 5. Groba, J.: Parasites of fish. — 6. Spodniewska, I. and Hillbricht-Ilkowska, A.: Biomass and production of phytoplankton. — 7. Hillbricht-Ilkowska, A. and Węgleńska, T.: Numbers, biomass and production of the zooplankton. — 8. Hillbricht-Ilkowska, A., Prejs, A. and Węgleńska, T.: Approximate assessment of the utilization by fish of the biomass and production of zooplankton. — 9. Kajak, Z. and Dusoge, K.: Number and biomass of bot-

Some work has been completed. The results were published in *Ekologia Polska* under the common title 'Experimentally increased fish stock in the pond-type Lake Warniak' (Spodniewska and Hillbricht-Ilkowska 1973).

In my report I shall concentrate upon the comparison between phytoplankton structure, biomass and production in the first three years when benthophagous fish stock was introduced and, in the subsequent two years, when the lake was not stocked with fish.

It should be noted that the intensity of phytoplankton studies varied in the different years. The most intensive studies (once a week) were conducted in 1967 in three sites in parts of the lake previously differing in fish stock; the less intensive research (once a month) was made in the subsequent years.

There were no differences in phytoplankton composition and quantity in the different parts of the lake.

The phytoplankton biomass in Lake Warniak was generally low with comparatively slight variations in time (Fig. 1). No water blooms were observed during either study period. Maximum phytoplankton biomass was recorded in the different periods of the particular year of study in each case being due to the development of various algal groups. In the first three years, i.e. during the introduction of benthophagous fish, a comparatively high proportion of the blue-green algal biomass to total phytoplankton biomass was observed (20–35 per cent); dinoflagellates were also comparatively abundant, especially during the first two years. Green algae and diatoms occurred sporadically. In 1970 and 1971, with the fish stock being low, the average phytoplankton biomass was nearly the same as in the years with high fish stock, but a pronounced decrease in the blue-green algal biomass was recorded and an increase in dinoflagellate biomass (Table 1).

When the proportions of planktonic algae of different size are compared the variations of the phytoplankton community structure are apparent. The lowest contribution of nannoplankton to the whole phytoplankton biomass was recorded in the first year (about 40 per cent). In the subsequent two years an increase in the contribution of nannoplankton to the total algal biomass was recorded (70 and 61 per cent, resp.). First it was supposed to be an effect of increased fish stock on the lake biocenosis but the maximum proportion of nannoplankton forms was observed in the final two years of research (88 per cent in 1970, and 75 per cent in 1971) when the fish stock was the lowest (Table 1).

The highest average phytoplankton biomass and production were recorded in the first year, the introduced fish stock being the lowest. The phytoplankton biomass was about 5 mg per litre of fresh algal weight, the gross production during May–October was about 2,000 kcal per $m^2$. In the subsequent years, the introduced fish stock being higher, a decrease both in the biomass and

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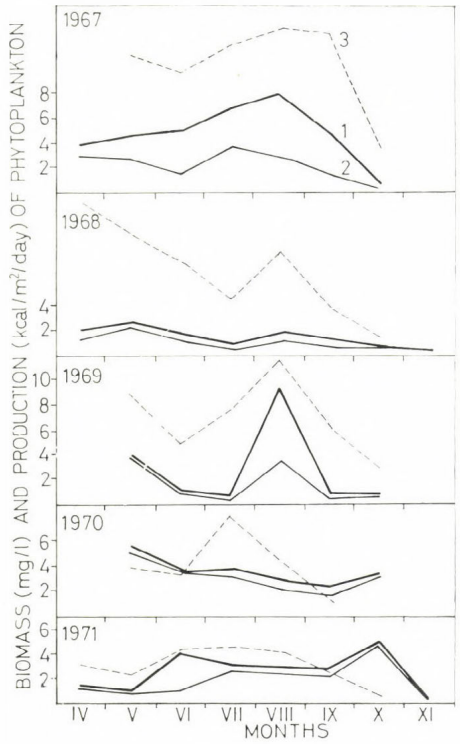


Fig. 1. Total phytoplankton biomass (1), biomass of nannoplankton (2) and gross phytoplankton production (3) in the pond-type Lake Warniak in successive years

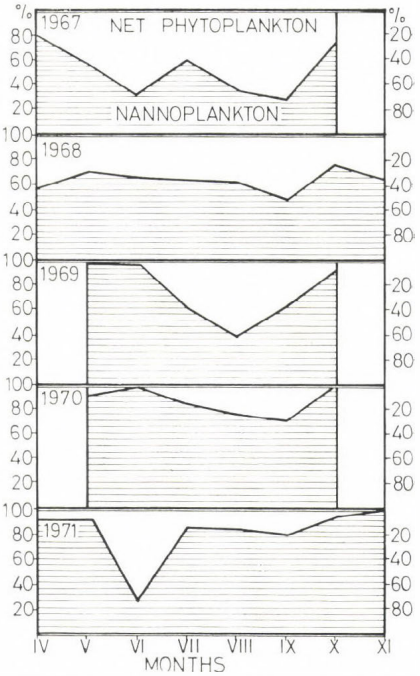


Fig. 2. Seasonal changes in phytoplankton structure in the pond-type Lake Warniak in successive years

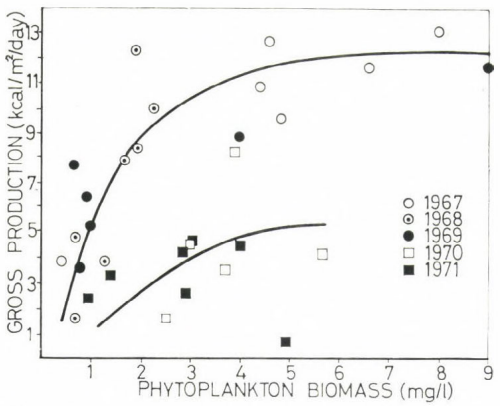


Fig. 3. Correlation between phytoplankton biomass and gross production in the pond-type Lake Warniak in successive years

production of phytoplankton was observed (Table 2; Fig. 3). Phytoplankton biomass was higher in 1969 than in 1968 probably owing to an exceptionally low water level but it had no significant effect on production.

In 1970 and 1971, when the lake was not stocked with fish, practically no fish from the previous introductions were present, the phytoplankton production was very low and the index of photosynthetic activity ($P/B$)

TABLE 1

*Average (May–October) biomass of different groups of phytoplankton and their contribution to the total phytoplankton biomass in the pond-type Lake Warniak in successive years*

| Year | Total phyto-plankton biomass | Nanno-plankton | | Net plankton | | Diatoms | | Blue-green algae | | Dinofla-gellates | | Green algae | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | mg/l | mg/l | % | mg/l | % | mg/l | % | mg/l | % | mg/l | % | mg/l | % |
| 1967 | 4.8 | 2.0 | 42 | 2.8 | 58 | 0.20 | 5 | 0.99 | 21 | 1.10 | 26 | 0.65 | 14 |
| 1968 | 1.5 | 1.1 | 70 | 0.4 | 30 | 0.03 | 2 | 0.50 | 32 | 0.34 | 27 | 0.03 | 2 |
| 1969 | 2.8 | 1.7 | 61 | 1.1 | 39 | 0.07 | 3 | 0.96 | 35 | 0.22 | 8 | 0.05 | 2 |
| 1970 | 3.7 | 3.3 | 88 | 0.4 | 12 | 0.18 | 5 | 0.14 | 4 | 1.20 | 33 | 0.05 | 1 |
| 1971 | 3.2 | 2.4 | 75 | 0.8 | 25 | 0.04 | 1 | 0.16 | 5 | 0.70 | 22 | 0.01 | 1 |

TABLE 2

*Biomass and production of phytoplankton and decomposition of organic matter in the water of the pond-type Lake Warniak in years of different fish stock*

| Year | Biomass of introduced fish | Average phyto-plankton biomass | Gross production of phytoplank-ton | $P/B$ | Decomposition (in per cent of gross pro-duction) |
|---|---|---|---|---|---|
| | kg/ha | mg/l | kcal/m²/year | | |
| 1967 | 40 | 4.8 | 2,000 | 1.6 | 67 |
| 1968 | 63 | 1.5 | 1,100 | 2.6 | 108 |
| 1969 | 62 | 2.8 | 1,300 | 1.9 | 89 |
| 1970 | — | 3.7 | 680 | 0.7 | 121 |
| 1971 | — | 3.2 | 570 | 0.8 | 119 |

was also low although there was a large proportion of nannoplankton to total biomass, usually having a high $P/B$ ratio (Table 2).

The highest maxima of the total algal biomass were recorded in 1967 and 1969 (about 15 mg per litre and 10.0 mg per litre of fresh weight, resp.). It should be noted, however, that the probability of finding the maxima of biomass was higher in the first year than later because of the higher frequency of sampling. In the other years no significant changes in the biomass of the various groups of algae were observed except for a high diatom biomass in the first year. Maximum nannoplankton biomass averaged 5 mg per litre fresh algal weight for several years, being almost 3 times higher but only in the first year (Table 3).

TABLE 3

*Comparison of maximal values of biomass of different groups of phytoplankton in the pond-type Lake Warniak in successive years*

| Year | Total phyto-plankton biomass | Nanno-plankton | Diatoms | Blue-green algae | Dinoflagel-lates | Green algae |
|---|---|---|---|---|---|---|
| | mg/l | mg/l | mg/l | mg/l | mg/l | mg/l |
| 1967 | 15.2 | 13.4 | 6.3 | 4.7 | 7.0 | 6.9 |
| 1968 | 4.8 | 4.9 | 0.2 | 0.9 | 1.6 | 0.3 |
| 1969 | 10.5 | 4.6 | 0.3 | 6.1 | 0.7 | 0.3 |
| 1970 | 6.7 | 5.9 | 0.7 | 0.7 | 3.5 | 0.3 |
| 1971 | 6.3 | 4.7 | 0.3 | 0.7 | 6.1 | 0.1 |

Analysis of seasonal changes in phytoplankton structure generally indicates that the contribution of nannoplankton to total phytoplankton biomass is higher in spring and autumn (even above 90 per cent of biomass); the comparison of the results from the successive years of study indicated that the importance of this group of algae in Lake Warniak had gradually been increasing (Fig. 2).

Considerable differences were found in the total gross phytoplankton production in the May–October period in the different years of the research (Table 2). The phytoplankton production was higher in the years when not only autochthonous but also introduced fish stock was present in the Lake (though it decreased in the successive years) than in the two subsequent years of investigation (Fig. 1, Table 2).

As it has already been mentioned, the highest production (about 2,000 kcal per $m^2$ per year) was found in the first year when also the biomass of phytoplankton was the highest. A slightly lower production was found in 1968 and 1969 (above 1,000 kcal per $m^2$ per year), and very low production in the two final years (570 and 860 kcal per $m^2$ per year, resp.).

This situation might be a result of the limiting effect of the increased fish stock, in the years of fish introduction, on phytoplankton production (worsening of environmental conditions, mainly of light conditions).

During the final two years, with the fish pressure decreasing, the conditions for macrophytes similarly improved. This could result in the decrease of phytoplankton production because of a competition between macrophytes and algae. Simultaneously, the lower pressure of fish on zooplankton could indirectly limit the phytoplankton development (increase in zooplankton grazing).

A pronounced increase was recorded in the organic matter decomposition in lake waters during successive years of research, which could have been due to changes in fish activity (fish roiling, a factor accelerating organic matter decomposition) in the first years, and probably to zooplankton activity in the final years.

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*Symp. Biol. Hung.*, *15*, pp. 109–112 (1975)

# JÄHRLICHE PRIMÄRPRODUKTION DER MAKROPHYTENÖKOSYSTEME IM BALATON

von

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Unsere bisherigen Forschungen, in denen die ökologischen, zönologischen und sukzessionsdynamischen Diszipline verwendet wurden, führten zu nützlichen neuen Aufklärungen bei der Auswertung der Produktionsbiologie (I. Kárpáti und Varga 1970, I. Kárpáti u. Mitarb. 1971).

Die Untersuchungen wurden im Balaton, in der Keszthelyer und Szigligeter Bucht in den folgenden Assoziationen durchgeführt:

1. *Myriophyllo-Potametum potametosum perfoliati*
2. *Trapetum natantis*
3. *Ceratophylletum demersi*
4. *Myriophyllo-Potametum myriophylletosum spicati*
5. *Scirpo-Phragmitetum schoenoplectetosum lacustris*

Bei der Probenentnahme von Laichkraut wurde neben der Probeflächengröße auch die Wassertiefe gemessen. Die Wassertiefe wurde in folgende Gruppen eingeteilt:

| | | | |
|---|---|---|---|
| A | 0– 50 cm | D | 150–200 cm |
| B | 50–100 cm | E | 200–250 cm |
| C | 100–150 cm | F | 250–300 cm |

Nach der Schätzung des Deckungsgrades und der genauen Messung der Wassertiefe wurde die gesamte Laichkrautmasse aus dem Rahmen für die Probenentnahme mit der Hand herausgenommen. Bis 2–2,5 m Wassertiefe konnte bei der erforderlichen Genauigkeit diese Methode benützt werden. Die herausgenommenen Proben wurden in Gaze eingepackt, das Volumen gemessen, sodann frisch, lufttrocken und absolut trocken gewogen. Mit diesen Grunddaten lassen sich folgende ökologische Auswertungen und Berechnungen vornehmen.

1. Zusammenhang zwischen Deckungsprozent, Wassertiefe und Phytomassenproduktion.
2. Phytomassenproduktion der Musterfläche.
3. Zusammenhang zwischen Frisch- und absolutem Trockengewicht.

Die aus zahlreichen Wassermonolithen gewonnenen Daten helfen die durchschnittliche Phytomassenproduktion der einzelnen Pflanzengesellschaften in bestimmter Lage und im gegebenen Vegetationsjahr zu ermitteln.

Parallel mit der Messung der jährlichen Phytomassenproduktion wurden Vegetationskarten angefertigt.

Über die Methoden der Wasser- und Ufervegetationskartierung stehen in der Literatur nur wenige Arbeiten zur Verfügung. Neben einigen mit überlieferten (geodätischen) Methoden angefertigten Karten ist uns nur die Arbeit Langs (1964) bekannt, die die Vegetationskomplexe und Zonationen mit Luftaufnahmen darstellt.

Die erste Phase der Forschungen bildete die geodätische Aufkartierung der Pflanzengesellschaften in den ständig und zeitweilig von Wasser bedeckten Lagen. Nach den botanischen Aufnahmen der Laichkrautgesellschaften und Schilfzonen in ihrer optimalen Entwicklung (Ende August), wurde die Kartierung begonnen, wobei folgende Daten berücksichtigt wurden:

*a)* Bedeckungsgrad des Bestandes in %,
*b)* Maße des Flecks (Breite, Länge, Form),
*c)* die Fläche der Flecken,
*d)* die Wassertiefe am Peilungspunkt.

Dann wurde von der Musterfläche, die von der Uferlinie umschlossen war, ein geodätisches Festpunktnetz eingerichtet. Von der Meßstation aus wurden die Messungen mit numerischem Vorwärtseinschnitt bestimmt.

Zweifellos ist der photogrammetrische Weg der modernste, den auch wir bereits benützen. Die methodischen Studien zu den Luftaufnahmen begannen im Jahre 1968 und zum Versuch wurden einige Aufnahmen gemacht, die zur Beurteilung der geodätischen Methoden sehr nützlich waren. Zur Zeit steht leider nicht jedem Botaniker ein Flugzeug zur Verfügung.

Seit drei Jahren verwenden wir stets die Luftbildaufnahmen. Die Bildflüge wurden jahreszeitlich jeweils auf den optisch günstigsten Vegetationszustand abgestimmt, ebenso auf gute Witterung und geeignete Tageszeit, was z. B. zur Vermeidung von Wasserspiegelungen wichtig ist.

Zunächst wurde von den zahlreichen Methoden und Kombinationen (z. B. präzise einbildphotogrammetrische Vermessung, Kombination der geodätischen Vermessung mit der Kleinbildkamera) die beste ausprobiert. Selbstverständlich hat jede Methode ihre Vorteile und stößt auch auf Schwierigkeiten bei der Lösung der Aufgabe.

Als Basiskarten dienen die aus größeren Höhen mit der Meßkamera exponierten auf 1 : 10 000 (1 : 5 000) transformierten Photokarten. Von den interessanten Details wurden Luftbildaufnahmen aus 200–500 m Höhe mit der Kleinbildkamera angefertigt. Aus den ausprobierten Methoden wurde von uns die Kombination der Photopläne mit den Kleinbildaufnahmen gewählt.

Das Wesen dieser Kombination der genauen Photokarten mit den Kleinbildaufnahmen besteht darin, daß bei dieser Methode zur Erstellung eines Photoplanes Aufnahmen herangezogen werden können, die für einen anderen Zweck angefertigt worden sind. An den Stellen aber, wo die Aufnahmen nicht im günstigsten Vegetationszeitpunkt vorgenommen worden waren und daher einzelne Details nicht zufriedenstellend zu erkennen sind, läßt sich der Plan durch Aufnahmen ergänzen, die mit einer Kleinbildkamera aufgenommen wurden.

So lassen sich mit der Basiskarte und einer normalen Kleinbildkamera in der optimalen Vegetationszeit mehrere Serien herstellen und der Maßstab der vorhandenen Photokarte läßt sich vergrößern.

Aus den Daten der Vegetationskarten und »Wassermonolith«-Probenaufnahmen wird die Phytomassenproduktion der Vegetation in der kartierten Lage errechnet.

Die folgenden Angaben wurden von der Keszthelyer Bucht (1969) und von der Szigligeter Bucht (1970) ermittelt:

| | Keszthelyer Bucht | Szigligeter Bucht |
|---|---|---|
| Mit Laichkraut bedeckte Fläche: | 308,349 ha | 108,597 ha |
| Davon mehr als 1% bedeckt: | 51,337 ha | 42,237 ha |
| Davon unter 1% bedeckt: | 57,102 ha | 66,359 ha |
| Laichkrautbedeckte Fläche bezogen auf die gesamte Wasserfläche (1327,4 ha) | 9,4% | 8,1% |
| Schilfbedeckte Fläche (132,1 ha) bezogen auf die offene Wasserfläche | — | 10,0% |
| Durchschnittliche grüne Phytomassenproduktion eines 1 m² großen Musterabschnitts mit mehr als 1% bedeckter Laichkrautfläche | 0,3 kp | 1,3 kp |
| Durchschnittliche grüne Phytomassenproduktion eines 1 m² großen Musterabschnitts mit weniger als 1% bedeckter Laichkrautfläche | 0,05 kp | 0,07 kp |
| Grüne Phytomassenproduktion der Szigligeter Bucht während eines Jahres | 281 000 kp | 575 957 kp |
| Absolutes Trockengewicht der gesamten Laichkrautproduktion | | 63 355 kp |
| Verhältniszahl der gesamten grünen Laichkrautproduktion und der gesamten Wasserfläche | 0,0085 kp/m² | 0,043 kp/m² |

Neben den obigen wertvollen Daten der Luftaufnahmeninterpretation einer Wasserlandschaft und den Phytomassenproduktionsbestimmungen vermag man mit diesem Verfahren auch Anhaltspunkte zur Lösung der wasserwirtschaftlichen Aufgaben, vor allem der biotechnischen Fragen zu gewinnen.

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*Symp. Biol. Hung.*, *15*, pp. 113–123 (1975)

# GROWTH AND MINERAL NUTRIENTS IN SHOOTS OF *TYPHA LATIFOLIA* L.

by

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## INTRODUCTION

*Typha latifolia* L. is a helophyte which frequently occurs in marshes and shallow waters with fluctuating water level. Owing to its rapid spreading, this species tends to be among the first reedswamp plants to invade such water bodies in the Pannonian region of Europe (Hejný 1960). Several years ago, favourable conditions for the establishment of *Typha latifolia* arose at the former Lake of Kobylí, once a shallow and marshy lake which had been eventually drained and turned into arable land in about 1840 and became partly reflooded and recolonized by wetland vegetation during the years 1960–67. The area of the former Lake of Kobylí (lat. 48°58′ N., long. 16°55′ E., alt. 185 m) is situated in South Moravia, at the northern edge of the Pannonian basin. In 1965–67, its plant life was investigated within the Czechoslovak IBP projects PT/4 and PP/3 (see IBP News nos 13 and 14) by members of the present Departments of Ecology and Hydrobotany of the Botanical Institute of the Czechoslovak Academy of Sciences, in Brno and Třeboň, respectively.

*Typha latifolia* played a key role in the reconquest of the flooded arable land by reedswamp and formed continuous and nearly pure invasion stands covering large areas (for further details see Fiala and Květ 1971). A selected *Typha latifolia* stand was subjected to analysis of growth and canopy structure during the growing season of 1966 (Květ et al. 1969, Květ 1971). The present paper, while referring to some of these results, mainly deals with the accumulation of the principal macronutrients: N, P, K, Ca, Mg and Na and total ash in the above-ground parts (shoots) of this *T. latifolia* stand.

## MATERIAL AND METHODS

The *Typha latifolia* stand occurred in that part of the former Lake of Kobylí which had been flooded for several years prior to 1966. The results of the analyses of water (performed by Dr. K. Fiala) and soil (of samples taken in the autumn of 1966) given in Table 1, illustrate the trophic conditions of the site. The easily soluble cations ($K^+$, $Na^+$) appear to have been leached from the soil into the water. The eutrophic character of the habitat as well as its slight salinity (about 0.13 per cent) are evident. During the 1966 growing season, the depth of the water varied between −35 and −70 cm. The fundamental macroclimatic characteristics of South Moravia have been described, e.g. by Dykyjová and Květ (1970). The methods of analysing

TABLE 1

*Results of anauyses of water (performed by Dr. K. Fiala on 17.11.1965) and soil (sampled in autumn 1966 at two depths) from the site of the Typha latifolia stand investigated. The soil was a heavy clay loam (alluvial silt deposit). The contents of the elements P to Fe in the soil have been estimated in an extract with 1 per cent citric acid ('available' nutrients)*

| Water | | Soil | | |
|---|---|---|---|---|
| | | Depth | 0 to —20 cm | —20 to —40 cm |
| pH | 7.0 | pH | 7.8 | 8.0 |
| Alkalinity, mEq/l | 11.90 | pH in KCl | 7.0 | 7.0 |
| Acidity, mEq/l | 0.75 | carbonate, % | 10.6 | 11.1 |
| Total hardness, degree | 72.3 | C% | 3.40 | 2.06 |
| $Ca^{2+}$ ppm | 453.3 | total N % | 0.30 | 0.24 |
| $Mg^{2+}$ ppm | 38.3 | P % | 0.005 | 0.0015 |
| $Na^{+}$ ppm | 125.0 | K % | 0.027 | 0.017 |
| $K^{+}$ ppm | 29.0 | Ca % | 1.76 | 0.73 |
| $Cl^{-}$ ppm | 199.5 | Mg % | 0.17 | 0.08 |
| $PO_4^{3-}$ ppm | 1.49 | Na % | 0.019 | 0.009 |
| $SO_4^{2-}$ ppm | 434.5 | Fe % | 0.026 | 0.026 |
| | | $R_2O_3$ % | 0.296 | 0.192 |

the growth and canopy structure of this stand are described by Květ et al. (1969). The chemical analyses of the biomass were made according to Koppová et al. (1955): Na — after Kjeldahl; P — colorimetrically with molybdenum blue; K, N — by flame photometry; Ca, Mg — complexometrically; ash is expressed as the sum of the above elements (except N) plus 'residual' ash (chemically unspecified residue on the filter, mainly $SiO_2$). The shoot biomass to be analysed had been harvested in a stratified manner — by 40-cm horizontal layers — on 6.6., 4.8. and 28.9.1966. The samples from each layer were divided into the following components: leaf bases with stems, leaf blades (hence called 'stems' and 'leaves', resp.) and inflorescences (in their respective stages of development). Separate analyses were made of the 'stems' and 'leaves', wherever present, sampled from the individual 40-cm horizontal stand layers; only in a few instances were the results of analyses of the material from one layer also applied to a neighbouring layer. Most of the analyses of the 'stems' were made separately for flowering and non-flowering shoots but in this paper these two kinds of shoots are not distinguished. Data presented here on the chemical constitution of the 'stems' have been obtained by an approximative extrapolation based on the knowledge of the synmorphology of the stand. The chemical analyses have yielded data which are expressed in terms of the percentage contents of the individual mineral constituents in the dry weight of the biomass (oven-dried at 80 °C to 90 °C). These percentage contents and the respective biomass values have been used to calculate the approximate amounts of each mineral constituent in the stand per 1 $m^2$ of ground area.

Most of the primary biomass data have been sampled by Dr. J. Svoboda who also prepared the samples for chemical analyses. The biomass and soil analyses were accomplished at the laboratories of the Forestry Research

Institute, Station Opočno, under the supervision of Mr. J. Vacek. The author's most sincere thanks go to both of them as well as to other colleagues who kindly assisted in this work.

## RESULTS

*Growth and biomass.* The growth curves of shoot biomass, leaf area index and time changes of density of the *Typha latifolia* stand are given by Květ et al. (1969). The stand continued its growth—with both the average shoot size and density increasing—till late September, only the leaf biomass decreased slightly between 4.8 and 28.9.1966 mainly due to the death of the leaves of the fertile shoots. The final total shoot biomass was 1,620 g $m^{-2}$ at a stand density of 28.7 shoots $m^{-2}$, which on 6.6 had been only 17.5 sh. $m^{-2}$. The average rate of net increase in shoot biomass was 9.4 g $m^{-2}$ $d^{-1}$ over the whole growing season. The maximum leaf area index of 3.2 (one side of the leaves in horizontal projection) was attained on 4.8. and persisted till 28.9, the loss of the relatively heavy leaves of the fertile shoots having been balanced by the formation of new thinner and relatively lighter leaves, especially on the newly emerging young offshoots. The maximum stand height was about 230 cm. In high summer, some 15 to 20 per cent of the shoots were flower-bearing. Figure 1 illustrates the vertical arrangement of the shoot biomass on the three dates of sampling for chemical analyses. It follows from the structural features of the *T. latifolia* shoots that 'stems' in the two bottom layers mostly include aerenchymatous leaf bases whereas real stems predominate in the layers higher up. Most of the steeply inclined leaf blades of *T. latifolia* cut across several horizontal stand layers: hence the 'leaves' in the lower stand layers mostly include the relatively thick aerenchymatous basal parts of the blades, whereas the upper layers most of the thin leaf tips. The inflorescence biomass is mostly concentrated in the 160–200-cm layer.

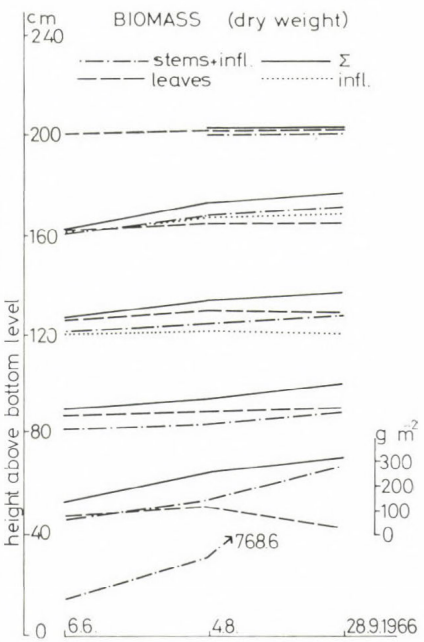



Fig. 1. Biomass of the 'stems' with inflorescences, 'leaves', inflorescences alone and total shoot biomass in individual 40-cm horizontal layers in the *Typha latifolia* stand on the three dates of sampling for chemical analyses

*Nitrogen.* Figure 2 shows the vertical distribution of N in the shoots on the three sampling dates. The percentage N content in the 'leaves' evidently increases from the bases to tips, with only small seasonal differences in both the percentage N content and the amount of N in the leaves per 1 $m^2$, presumably because of the continuous emergence of new young leaf blades.

The percentage N content in the inflorescences is rather high. Although the percentage N content in the 'stems' is low the basal parts of the shoots contain a rather large amount of N per 1 m² because of the high 'stem' biomass present in the 0–80-cm stand layers. This feature stands out particularly clearly towards the end of the growing season (28.9). In summer and autumn, the total amount of N in the stand shows a distribution with one peak in the bottom stand layers and another peak in the 160–200-cm layer. Large amounts of N are thus either returned to, or removed from,

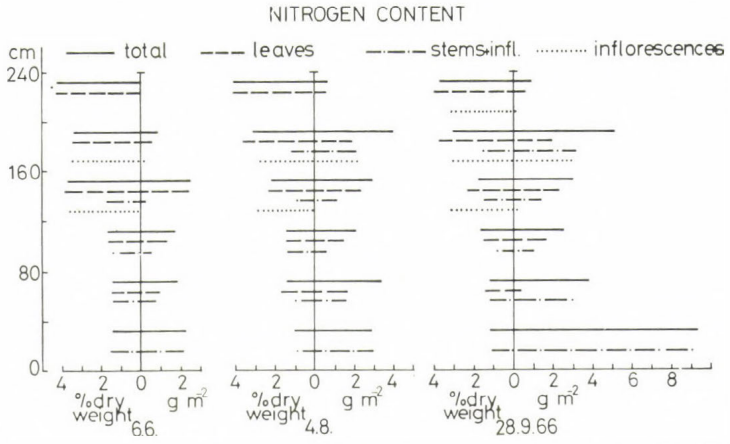
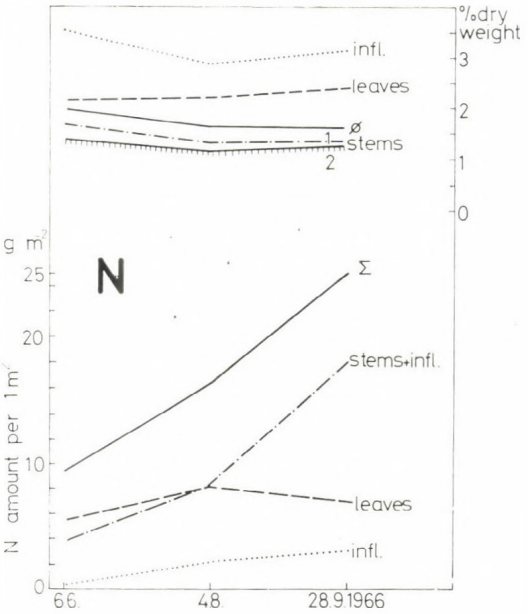



Fig. 2. Percentage nitrogen content and its amounts per 1 m² in the total shoot biomass, 'stems' with inflorescences, 'leaves' and inflorescences alone, in individual 40-cm horizontal layers on three dates during the main growing season

the habitat when *Typha* is cut at some 30 to 50 cm above bottom level in summer to autumn and is either left to decompose on the spot (which is common practice in fishpond management in order to control the width of the reed belt) or is taken away to be used commercially (mostly in domestic industries). Similar diagrams showing their vertical distributions can also be drawn for other mineral elements included in this paper, and are available on request from the author. Figure 3 summarizes the data given in Fig. 2 and illustrates the high average net uptake rate of N by the stand throughout the main growth period (nearly 0.14 g $m^{-2}$ $d^{-1}$). The decrease in 'leaf' biomass is apparently responsible for the slight decrease in the amount of N stored in the 'leaves' in late summer.

*Phosphorus* (Fig. 4). Apart from the substantially lower P level, both the vertical distribution and overall time changes of the P content follow a similar pattern as those of the N content. The marked decrease of the percentage P content in the inflorescences (in which, however, the P concentration remains higher than in the other organs) is apparently connected with their decreasing physiological activity from budding to maturity. Despite the low share of inflorescences in the total biomass on both 4.8 and 28.9 (about 10 per cent and 6 per cent, resp.), their P content represents about 1/5 of the total P contained in the stand. The overall P concentration in the leaves remains fairly constant from June to September. Contrary

Fig. 3. Nitrogen content in the above-ground parts of the *Typha latifolia* stand. Top: Changes with time in the percentage (% dry weight) average content of N in the various shoot components indicated (for 'stems': 1, with inflorescences; 2, 'stems' only) and in total shoot biomass (Ø). Bottom: Time changes in total amounts of N contained in the various shoot components indicated and in total shoot biomass per 1 m² ground area



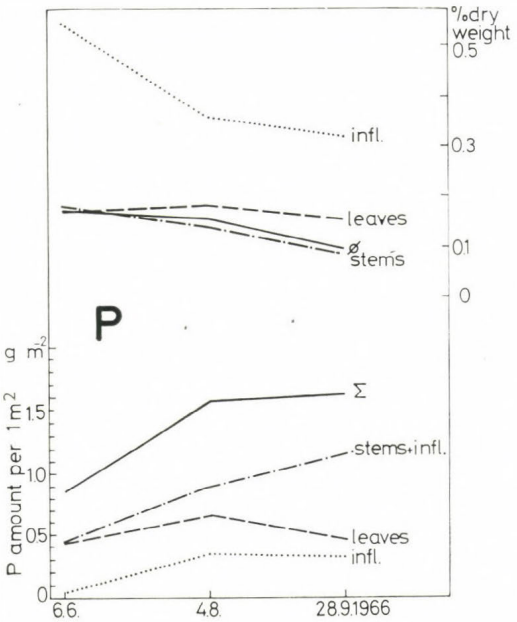




Fig. 4. Phosphorus content. Description as in Fig. 3. Percentage P content in 'stems' — 'stems' only

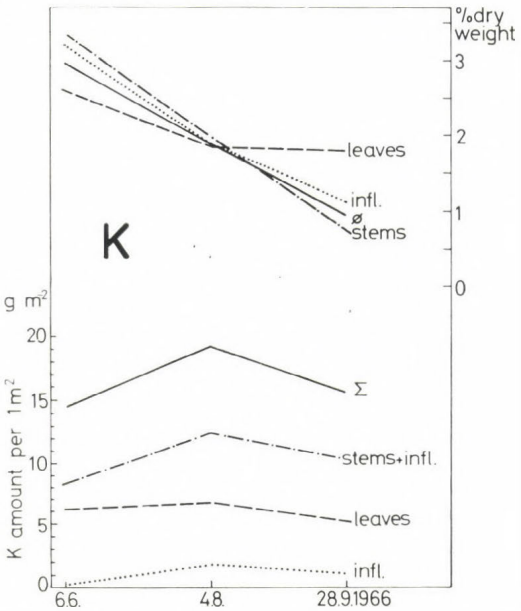



Fig. 5. Potassium content. Description as in Fig. 3

to N, however, most of the P uptake by the shoots takes place only in the first part of the main growing season.

*Potassium* (Fig. 5). The percentage content of K is rather evenly spread vertically in the stand on each of the three sampling dates, but with time the percentage K content in the shoots decreases, presumably with the gradually prevailing senescence of the individual shoot components. This overall decrease is partly checked but only in the leaves, probably because of the relatively higher K content in the leaves of the newly emerging offshoots. The amounts of K contained in the above-ground biomass (total as well as all its components) attain their maxima at the peak of the growing season. Later on, even the increase in biomass is incapable of balancing the decrease in the percentage K content. In this respect, K differs from all the other elements examined.

*Calcium* (Fig. 6). In the 'stems', the vertical distribution of Ca is fairly even on each sampling date, while its percentage content gradually decreases during the season. In the 'leaves', the percentage content of Ca decreases upwards (on 4.8, e.g., from 1.44 per cent at 40–80 cm to 0.68 per cent at 200–240 cm). The inflorescences contain conspicuously little Ca. Most of the Ca is stored in the 'stems', especially towards the end of the growing season although the percentage content of Ca remains higher in the leaves.

*Magnesium* (Fig. 7). In most plants, the percentage content of Mg tends to be relatively the highest in the leaves (chlorophyll). The high proportion of non-assimilatory aerenchyma and sclerenchyma in both the 'stems' and 'leaves' and the high Mg content in the ripening inflorescences somewhat obscure this feature in *T. latifolia*. Only the leaf tips, thin and rich in assimilatory tissue, contain up to 0.29 per cent of Mg and are thus distinctly Mg-richer than the other shoot parts. As a result, most of the Mg is contained in the stems and inflorescences during the whole growing season.

*Sodium* (Fig. 8). The content of this element is particularly interesting to follow at the somewhat saline Lake of Kobylí. As a rule, the lower stand layers show a several times higher percentage content of Na in both 'stems' and 'leaves' than the upper layers (e.g. the leaves on 4.8: 0.36 per cent at 40–80 cm and 0.07 per cent at 200–240 cm). This seems to indicate the association of higher Na concentration with non-assimilatory tissues. The seasonal course of the overall percentage content of Na seems to mirror, to a certain extent, that of the Ca content in all three shoot components analysed. The total amount of Na stored in the stand is relatively high, the stems containing most of it.

*Ash* (Fig. 9). The average percentage ash content seems to be fairly low in the *Typha latifolia* shoots and the ash content is rather evenly distributed vertically. It also evenly decreases during the growing season. This decrease seems to be associated with the increasing share of aerenchyma and mechanical tissue in the anatomical structure of the shoots. Most of the rather small amount of ash contained in the stand seems to be, however, physiologically active. The content of 'residual' ash (other than P, K, Ca, Mg, Na) is rather low during the whole growing season and increases from only about 0.14 per cent of dry weight on 6.6. to about 0.30 per cent (12 per cent of total ash) on 28.9. This 'residual' ash may be assumed to contain mostly $SiO_2$. Chloride and the physiologically important sulphur, iron and micronutrients have not been estimated as they were removed with the filtrate.

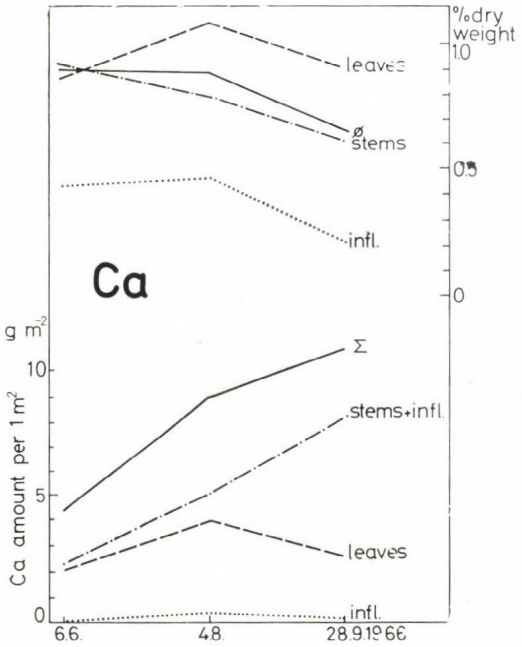



Fig. 6. Calcium content. Description as in Fig. 3

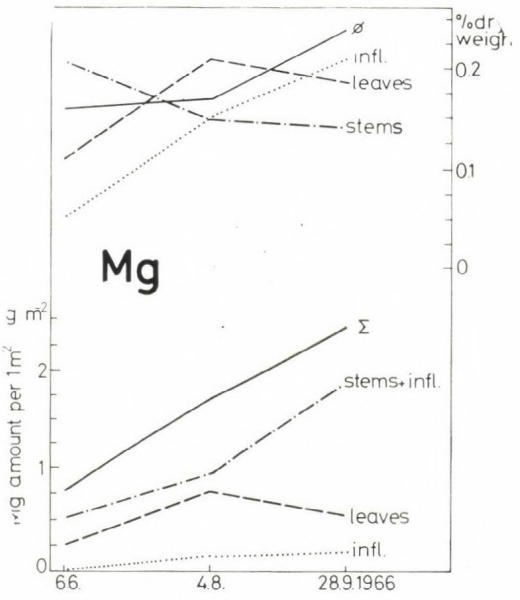



Fig. 7. Magnesium content. Description as in Fig. 3

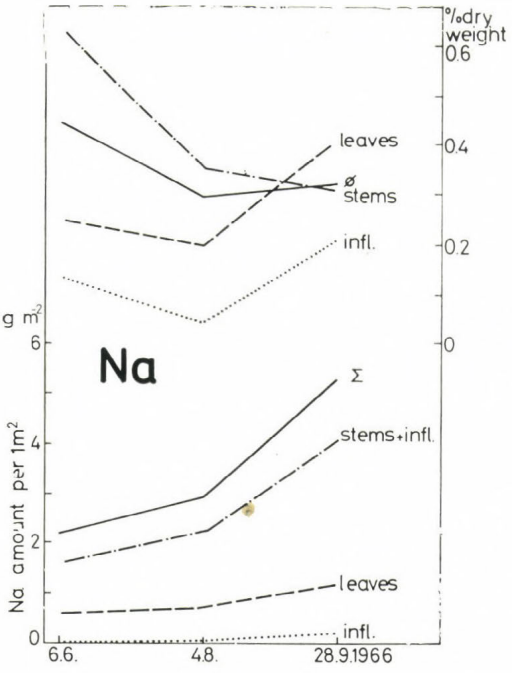



Fig. 8. Sodium content. Description as in Fig. 3

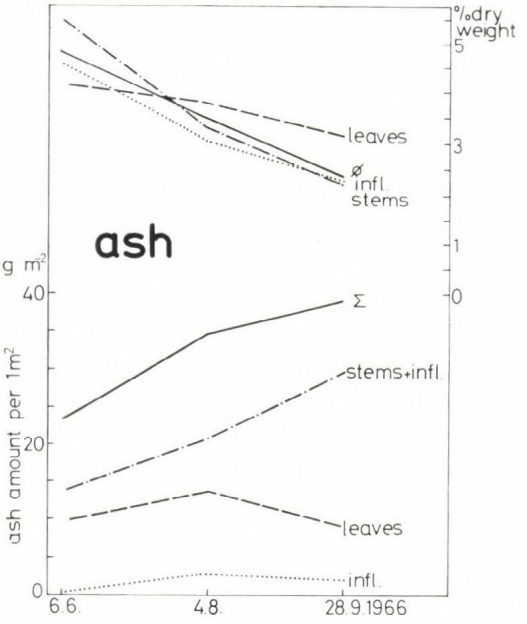



Fig. 9. Ash content. Description as in Fig. 3

## DISCUSSION

Our data on mineral nutrient content in the above-ground parts of the *Typha latifolia* stand are comparable with other data from the literature. Dykyjová (1973*a*) summarizes some of her own as well as other authors' data on the contents of macronutrients in *Typha latifolia*, *T. angustifolia*, *Phragmites communis* and other helophytes. A similar survey was published by Riemer and Toth (1968). Our data mostly fall within the ranges of the values given for *T. latifolia*. The Na content in our *T. latifolia* stand approaches the upper limit of the range evident from both surveys quoted. The mean percentage content of P (0.4 per cent) given by Riemer and Toth (1968), however, highly exceeds our values. These authors also surveyed the chlorine content in *T. latifolia* and arrived at a high mean value of 2.87 per cent Cl in its dry matter. The capacity of this species to store Cl and Na may serve as a useful tool for the purification and desalination of slightly brackish eutrophic water (see Boyd 1970*a*). Marsh (1955) reports on an ancient Egyptian practice of using *Typha* to clarify certain areas of the Nile delta of salt. The percentage contents of N, P, K and Ca in *T. latifolia* reported from northern Poland by Bernatowicz (1969) are lower than ours, the low ash content (5.11 per cent) found by him corresponds with our findings. Boyd and Hess (1970) conducted a special survey on shoot production and mineral levels in *T. latifolia* in the SE United States. Our percentage contents of the macronutrients are within the ranges stated by these authors. Boyd (1970*b*) found, in a probably less fertile habitat, lower contents of Ca and Na in *T. latifolia* than we did. In accordance with our results of 6.6.1966, the percentage content of K in his stand also surpassed that of N.

The great variation in the percentage contents of macronutrients reported in the literature points to the importance of examining seasonal changes as well as spatial distribution of the contents of mineral nutrients in aquatic and littoral vascular plants. The variation can also be better understood if it is related to the structural peculiarities, growth and development of the plants concerned.

Boyd (1970*c*, 1971) checked the seasonal changes in the percentage contents and total amounts of N, P and K in *Typha latifolia*. The percentages reported by him largely correspond with ours obtained on comparable dates but the total amounts are smaller as a result of the smaller biomass of his stand (Boyd 1970*c*). Stands of the closely related *T. angustifolia* have been examined in this respect by Husák (1971) on the South Moravian eutrophic and slightly saline Nesyt fishpond, and by Dykyjová (1973*b*) on the originally oligotrophic but nowadays eutrophicated Opatovický fishpond in South Bohemia. The seasonal courses of the percentage contents of N, P, K, Ca, Mg and Na in *T. angustifolia* did not substantially differ from those in *T. latifolia*, only the Ca content was appreciably lower at the Opatovický fishpond (Dykyjová 1973*b*).

Our results of the analyses of *Typha latifolia* shoots are also comparable with the analyses, performed simultaneously and using the same methods, of a well-developed (seasonal maximum biomass, 1,810 g $m^{-2}$) stand of *Phragmites communis* at the Nesyt fishpond (Květ 1973). In both *Typha* and *Phragmites*, the leaves were richer in mineral nutrients than the stems. The overall percentage N contents as well as amounts of N per 1 $m^2$ were

also similar. At the peak of the growing season, *Phragmites* was richer in P and K, and poorer in Ca, Mg and Na than *T. latifolia*. In *Phragmites*—in contrast to *Typha*—all the elements examined showed a steep fall both in their percentage contents and in the amounts stored per 1 $m^2$ after the peak of the growing season. Another difference was the somewhat higher ash content in *Phragmites* (about 6 per cent). By the end of the growing season, most of it became, however, 'residual' ash.

With respect to the trophic status of the habitat, *T. latifolia* seems to display great plasticity. This statement also applies to the Pannonian region of Europe (Hejný 1960). In South Moravia, lush and highly productive stands of *T. latifolia* are found in areas which are eutrophicated by domestic sewage or animals (e.g. geese, gulls). This is another sign of the tolerance of this species to an increased content of Na and Cl in the environment. Hejný and Husák (1973) classify these communities dominated by *T. latifolia* as a special variant of the association *Glycerietum aquaticae*. Appreciable differences, however, seem to exist between the mineral compositions of *Typha* and *Glyceria* (Dykyjová 1973*a*), and hence the variant with *T. latifolia* is likely to be characterized by a specific type of mineral cycling. Muskrats (*Ondatra zibethica*) have been found to feed preferably on *T. latifolia*, when available, rather than on any other helophytes (Pelikán et al. 1970). Maybe this preference is also connected with the peculiarities of its chemical composition.

This paper does not attempt to discuss the physiological problems of mineral nutrient uptake by *Typha latifolia*, its rates and efficiency, antagonisms and ratios between individual mineral elements. These problems will be discussed elsewhere as far as the rather crude methods used allow a more refined examination to be made on the basis of the results reported here. The mineral nutrients taken up or lost by the shoots need not necessarily come from, or go to, the water or soil; they may also be transported to or from the rhizomes. This transport has been proved for P and K in *Phragmites* by Roman et al. (1971). In *Typha*, whose rhizomes usually live shorter than those of *Phragmites* (Fiala 1973), this transport is perhaps less important.

Taking *Typha latifolia* as an example, this paper attempted to illustrate those seasonal changes in the nutrient content in emergent macrophytes which take place even during the main growing season. The importance of these changes has to be borne in mind in any theoretical or practical considerations on mineral nutrient uptake by the communities of these plants. The spatial distribution of the mineral nutrients in the communities is also to be taken into account, especially in considering their role in mineral cycles, their decomposition, grazing or harvesting.

## SUMMARY

An invasion stand of *Typha latifolia* L., occurring on flooded arable soil, at the former Lake of Kobylí in South Moravia, at the northern edge of the Pannonian basin, was studied for the seasonal changes in shoot biomass and the contents of N, P, K, Ca, Mg and Na and total ash. The biomass was harvested in a stratified manner (by 40-cm horizontal layers) and was

divided into that of the leaf bases + stems ('stems'), leaf blades ('leaves') and inflorescences. The seasonal maxima of shoot biomass (dry weight) and density were 1.6 kg $m^{-2}$ and 28.7 shoots $m^{-2}$, resp., and both were recorded on 28.9.1966. The average rate of shoot biomass increase, over the whole growing season, was 9.4 g $m^{-2}$ $d^{-1}$, the maximum leaf area index, in August to September, was about 3.2 (one side of the leaf blades in horizontal projection). The average samples for the mineral analyses were taken from the material harvested on three dates: 6.6, 4.8 and 28.9.1966. The percentage contents of the mineral constituents found in our material appear to fall within the ranges given by other authors for *T. latifolia*. The estimated total amounts of the mineral macronutrients investigated and being contained in the above-ground parts of the *T. latifolia* stand depended, to a great degree, on the shoot biomass. The following approximate maximum values (all in g $m^{-2}$) were attained: N: 25.1, P: 1.6, K: 19.3, Ca: 10.9, Mg: 2.4, Na: 5.3, ash: 38.9—all on 28th September, except for K on 4th August.

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*Symp. Biol. Hung.*, *15*, pp. 125–131 (1975)

# BIOLOGY OF DUCKWEEDS IN A PANNONIAN FISHPOND

by

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## INTRODUCTION

The Nesyt fishpond—area 322 ha, lat. 48°46′ N., long. 16°44′ E., alt. 175 m—is the largest of the South Moravian fishponds being situated in the phytogeographical district of Eupannonicum. Its average depth is only about 2 m, the substrates are mainly alluvial deposits. The slightly saline (about 0.1 per cent) and eutrophic water is fertilized and limed since the fishpond is managed to produce marketing fish. Detailed water analyses as well as other information on the fishpond are contained in Květ (1973). Reedswamp plant communities (of the alliances *Phragmition communis* and *Scirpion maritimi*) cover about 10 per cent of the fishpond's area, i.e. some 30 ha. The littoral of Nesyt and the dominant plant species of these communities such as *Phragmites communis*, *Typha angustifolia*, *Bolboschoenus (Scirpus) maritimus* have been studied within the Czechoslovak IBP projects PT/4 and PP-P/3 (see IBP News nos 13 and 14).

Synusia of floating macrophytes, namely duckweeds, often occur within the reed belt as well as on the surface of the 'lagoons' (i.e. small patches of open water within the reed belt). The association of *Lemnetum gibbae*, composed of pure *Lemna gibba*, prevails in the littoral of Nesyt. Occasionally, the association of *Riccietum rhenanae*, composed of *Riccia rhenana*, *Lemna trisulca* and *L. gibba*, covers small areas (for details see Rejmánková 1973*b*).

The aim of this study has been to learn about the seasonal dynamics of the duckweed populations in the littoral of Nesyt. The expansive growth of the duckweeds and their rapid decay indicate that they represent an important link in the energy flow and pathways of nutrient cycling in the littoral of the fishpond.

## PHENOLOGY

The phenological development of *Lemna gibba* was observed during the years 1971–73. A scheme of this development taking place during the principal growing period is shown in Fig. 1. The sequence of the individual phenological phases is as follows.

1. The germination of the seeds starts at the beginning of May. This finding is in contrast with the generally accepted opinion that duckweeds mostly hibernate in the form of vegetative fronds (turions). For the *Lemna gibba* community on Nesyt, the latter type of hibernation is of little importance since more than 80 per cent of the new fronds germinate from seeds

in spring. Germination continues up to the end of May. The first fronds formed are small and flat, usually, somewhat purplish; this is probably connected with the relatively low water temperatures (about 15 °C) usually prevailing during that period.

2. The first half of June is characterized by a rapid vegetative reproduction of the duckweeds and, consequently, a rapid growth of their populations. Newly formed fronds spread quickly on the water surface; most of them are still flat, but some gibbous forms occur and sporadic flowers are found.

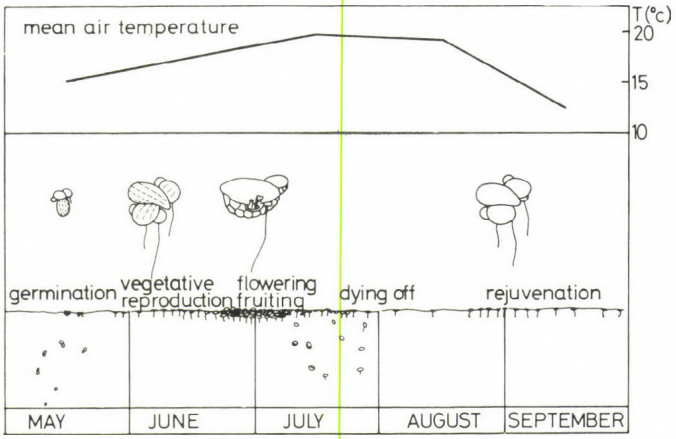


Fig. 1. Scheme of the phenological development of duckweeds (*Lemna gibba*) during the main growing season (May to September, abscissa). Upper part: monthly mean air temperatures at Lednice (4 km from Nesyt) in 1971 and 1972

3. The high growth rate of the populations leads to an overcrowding of duckweeds, which reaches its maximum at the end of June. Most fronds are gibbous at this time and most of them are flowering.

4. During the first half of July, the plants slowly start to die off, especially in densely overcrowded clusters. July is, as a rule, the warmest and sunniest month (see Fig. 1), and overheating of the thick duckweed cover appears to contribute to the rapid death of many fronds. By the beginning of August, hardly any living plants are left on the water surface.

5. During late August and September, the few remaining plants usually propagate again, but the growth rate never reaches the values observed at the beginning of the season. The fronds are mostly flat and they do not flower. These plants, usually, die during late October and November.

## GROWTH CHARACTERISTICS OF THE POPULATIONS

During the 1971–73 growing seasons, the following growth characteristics of the duckweed populations were investigated:

1. Relative growth rate (RGR) in the shade of canopies of emergent macrophytes (*Phragmites communis*, *Typha angustifolia*, *Bolboschoenus maritimus*) as compared with the RGR on unshaded open water.

2. Distribution of duckweed biomass along a line transect across the reed belt from open water towards the shoreline.

3. Biomass of the duckweeds at the time of their maximum development.

Rejmánková (1973*a*, *c*) gives a detailed description of the methods employed.

Figure 2 shows the seasonal changes in the average RGR of *Lemna gibba* growing in stands of different emergent macrophytes. This experiment was carried out at the eastern shore of Nesyt (for its characteristics see Fiala and Květ 1971), the depth of water varied between −40 and −60 cm.

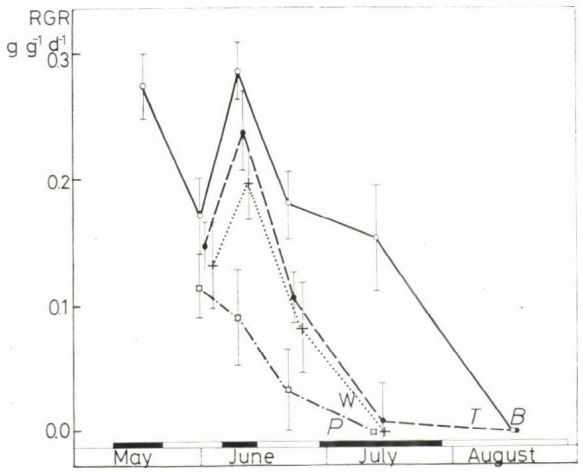


Fig. 2. Seasonal changes in the RGR (ordinate, g $g^{-1}$ $d^{-1}$) of *Lemna gibba* growing in stands of *Bolboschoenus maritimus* (*B*), *Typha angustifolia* (*T*), and *Phragmites communis* (*P*) and on unshaded open water (*W*). Nesyt fishpond, 1972. Abscissa: experimental intervals (black and white strips) and months from May to August

The best growth was recorded in the *Bolboschoenus* stand where the light and temperature conditions seemed to be most suitable for duckweed growth. Somewhat lower RGR values were observed in the *Typha* stand during the first three experimental intervals; later on the RGR decreased rather rapidly, apparently because of the increased shading of the duckweeds by *Typha*. The *Phragmites* stand was unusually dense (164 shoots per 1 $m^2$), which was reflected in the greatly retarded growth of the duckweeds present there. The RGR values of the duckweeds from the open water were also lower than could have been expected from experience with duckweed growth in unshaded open water in the 'lagoons' (see below and in the study of Rejmánková 1973*c*). The difference was mostly due to the lower temperatures of the open water as it also occurred in the reed belt.

Figure 3 shows the seasonal changes in the distribution of the duckweed biomass along a transect from open water towards the shore, across a dense stand of *Typha angustifolia*, a 'lagoon', a loose stand of *T. angustifolia*, a dense stand of *Phragmites communis* and a mixed *Ph. communis–Carex riparia* stand. The transect, 50 m long, was situated at the S. shore of Nesyt; for its characteristics see also Fiala and Květ (1971). At the beginning of the growing season, the depth of the water was −90 cm in the dense *T. an-*

*gustifolia*, and decreased to −20 cm in the *Phragmites–C. riparia* stand. In summer, the water level sank so that this stand became dry. The samples were taken at monthly intervals; for the methods used see Rejmánková (1973*c*). The RGR values were calculated from the dry weight changes in individual intervals. The initial biomass ($W_1$), used for the calculation of the RGR during the first interval, was assumed to be the same (= 0.2 g $m^{-2}$)

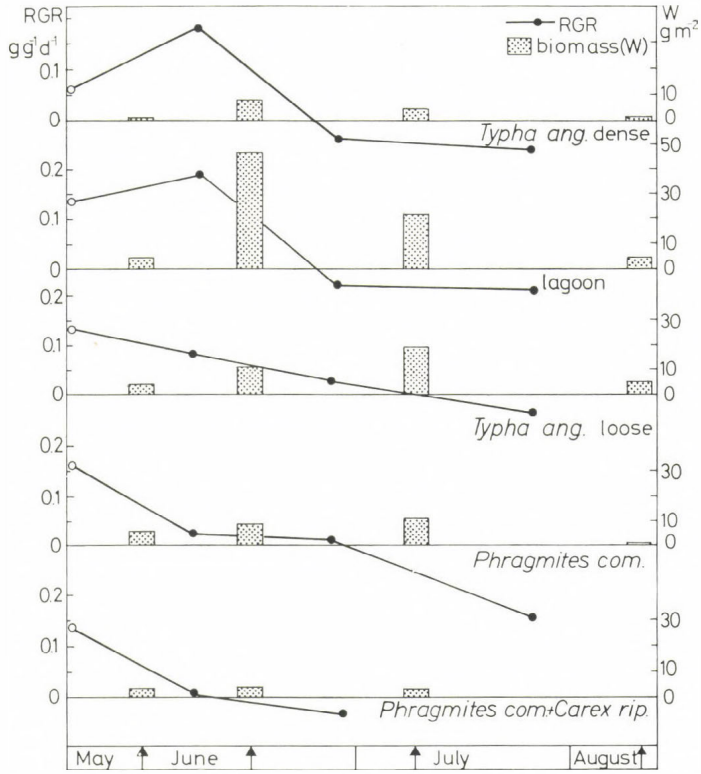


Fig. 3. Biomass (dry weight g $m^{-2}$) (columns) and RGR (g $g^{-1}$ $d^{-1}$) (full lines) along a transect from the dense stand of *Typha angustifolia* to a mixed stand of *Phragmites communis* and *Carex riparia*. Nesyt fishpond 1973. Abscissa: sampling dates (arrows)

at all the sites. This value had been derived from the number of fronds (= 1,000) present on the water surface at that time.

The RGR and biomass values can be related to the results of the phenological observations. The high RGR corresponds with the expansive growth in the first half of June, the dying off of the plants is the reason for the low biomass and negative RGR values in July. At the beginning of the growing season, hardly any differences existed in the growth of the duckweeds in the different stands; a slightly higher biomass was found only in the *Phragmites* stand, the shading effect of which did not play an important role at that time. In the middle of June, the duckweeds in the 'lagoon' showed the absolutely highest biomass recorded, and attained the seasonal maximum of their development. At the same time, somewhat lower seasonal maxima

were attained by the duckweeds in the dense *Typha* and in the *Phragmites–Carex riparia* stands. A marked decrease of duckweed biomass followed in these three stands. In the loose *Typha* stand, the duckweed biomass still continued to increase: the duckweeds were apparently less overcrowded there than in the 'lagoon' and the plants were also protected from unfavourable overheating. At the beginning of August, the duckweed biomass was very low in all the stands.

A similar example of the distribution of duckweed biomass along a transect from the thick duckweed cover on the water surface in a 'lagoon' across the reed belt towards the shore is shown in Fig. 4. The samples were taken


Fig. 4. Biomass of the duckweed synusium (columns) and relative radiation flux density ($I_0/I \cdot 100$, % *PhAR*, full line) along a transect from open water (W) to shore (abscissa, distance in metres) on 28.6.1971. The sketches show the structure of the reed stands

at the beginning of July 1972. The duckweed biomass decreased depending on the increasing density of the *Phragmites* and *Typha* stands. The shading effect of the emergent macrophyte stands is expressed in terms of the relative radiation flux density (*PhAR*) recorded at water level at noon on a day with overcast sky. An example of the range of the maximum biomass of duckweeds in different years is given in Table 1. In both 1971 and 1973, the water level in the fishpond was high, the fishpond being filled with water, without emerged shores. The markedly lower biomass values of 1973 result probably from the slower vegetative reproduction caused by low temperatures during spring. The *Bolboschoenus* stands did not develop their aerial

TABLE 1

*Values of the seasonal maximum biomass (dry weight, g $m^{-2}$) of duckweeds (Lemna gibba) recorded at the Nesyt fishpond during the years 1971, 1972 and 1973*

| Year | 'Lagoon' | *Typha ang.* loose | *Typha ang.* dense | *Bolboschoenus maritimus* |
|---|---|---|---|---|
| 1971 | 150 | 70 | 9 | — |
| 1972 | 20 | 85 | 12 | 80 |
| 1973 | 47 | 22 | 10 | — |

parts in these years, which is the reason for the absence of the respective duckweed biomass values. In 1972 the water level in the fishpond was low (about 50 cm, below the normal watermark). The duckweed biomass was high in the loose *Typha angustifolia* and *Bolboschoenus* stands. The low duckweed biomass in the 'lagoon' was probably caused by the competitive effect of filamentous algae, which strongly retarded the vegetative reproduction of duckweeds. At the beginning of that season, the water level was very low in the lagoon (about 10 cm). These conditions were suitable for the germination of such species as *Oenanthe aquatica*, *Ranunculus sceleratus*, *Veronica anagalis-aquatica*, *Potamogeton pectinatus*, etc. Later on, the water level rose by some 15–20 cm and all these plants served as a substrate for the growth of attached filamentous algae.

In all three years, the seasonal course of the growth characteristics of the duckweeds appeared to be much the same: the highest RGR and biomass values occurred during phase 2, of the rapid vegetative reproduction, with a high biomass persisting also through phase 3, of flowering and fruiting. The endogenous rhythm of a duckweed population development seems to be the main factor determining the seasonal course of the growth characteristics examined. The environmental factors seem to determine the range of their absolute values (see Table 1) without substantially altering the shape of the seasonal course.

The findings from the Nesyt fishpond cannot be directly extrapolated to other South Moravian water reservoirs. For example, the small fry-ponds situated in the vicinity of Nesyt being filled with the water coming from the Nesyt, are covered with a thick layer of the same duckweed species (*Lemna gibba*) during the whole summer. The phase of rapid vegetative reproduction continues also during the phase of flowering here, and the phase of massive dying off of the duckweeds does not take place. This difference might be caused by a lower degree of synchrony of the duckweed populations on the fry-ponds than that of the duckweed population on the Nesyt. The reason for this discrepancy is still unknown and requires further investigation.

The assessment of the biomass and growth rates of duckweeds on the Nesyt fishpond was the main task to be fulfilled. However low the biomass of the duckweeds may appear in comparison with that of the emergent macrophytes, its quick turnover during the growing season will significantly contribute to energy flow and nutrient cycling in the water. A close relationship between the development of duckweeds and changes in nitrogen and phosphorus compounds in the water within the reed belt of the Nesyt was found by Dvořák (1973). Low levels of phosphate (P) and ammonia (N) in the water, in May and June, corresponded with our phase 2 of the rapid vegetative growth of the duckweeds, and the rapid increase in these values in July and August corresponded with phase 4 of the duckweed dying off and decay.

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# II. BACTERIAL PRODUCTION AND DECOMPOSITION

*Symp. Biol. Hung.*, *15*, pp. 135–140 (1975)

# BACTERIA IN THE WATER AND MUD OF NEUSIEDLERSEE (AUSTRIA)*

by

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## INTRODUCTION

Because of a lack of information on bacteria in this very turbid, highly alkaline lake, except for some routine observations of the governmental pollution control station in Vienna being not available to me at the moment, it seemed to be of some interest for the IBP work on Neusiedlersee to obtain some information concerning bacterial biomass and production.

## METHODS

Total counts were made on Millipore filters (Membranfiltergesellschaft, Göttingen), pore size 0.2 $\mu$, stained with erythrosin. Biomass was calculated from cell counts and average cell volume (assuming a specific gravity of 1.0) and was converted to carbon by applying the formula of Kusnetsov and Romanenko (1966). Heterotrophic bacteria were enumerated on normal nutrient broth using the spread plate technique. Bacterial production was measured by means of $^{14}C$-uptake in the dark.

Estimates of microorganisms in the mud were made from core samples by direct microscopic counts and enumeration of viable cells on plates.

Decomposition processes were examined by use of BOD-bottles in the water and by determining the dehydrogenase activity in the bottom materials.

## RESULTS AND DISCUSSION

### *Biomass*

The range obtained for cell counts over two years was $0.69–1.78 \times 10^6$ for 1970 and $0.52–0.94 \times 10^6$ per ml for 1971. These values correspond to those of lowland lakes of meso- to slightly eutrophic character (Kusnetsov 1959, Overbeck 1968, Reinheimer 1971). They are comparable with measurements on Lake Balaton (Oláh 1969*a*, *b*) but much lower than, for instance, those from Lake Erken (Nauwerck 1963). Biomass increases slowly throughout the year reaching a peak in late autumn with minimum values during the

* Supported with equipments by grant No. 1637 of the *Fonds zur Förderung der Wissenschaftlichen Forschung* (Austria).

** Publ. No. 12 of IBP-PF Neusiedlersee.

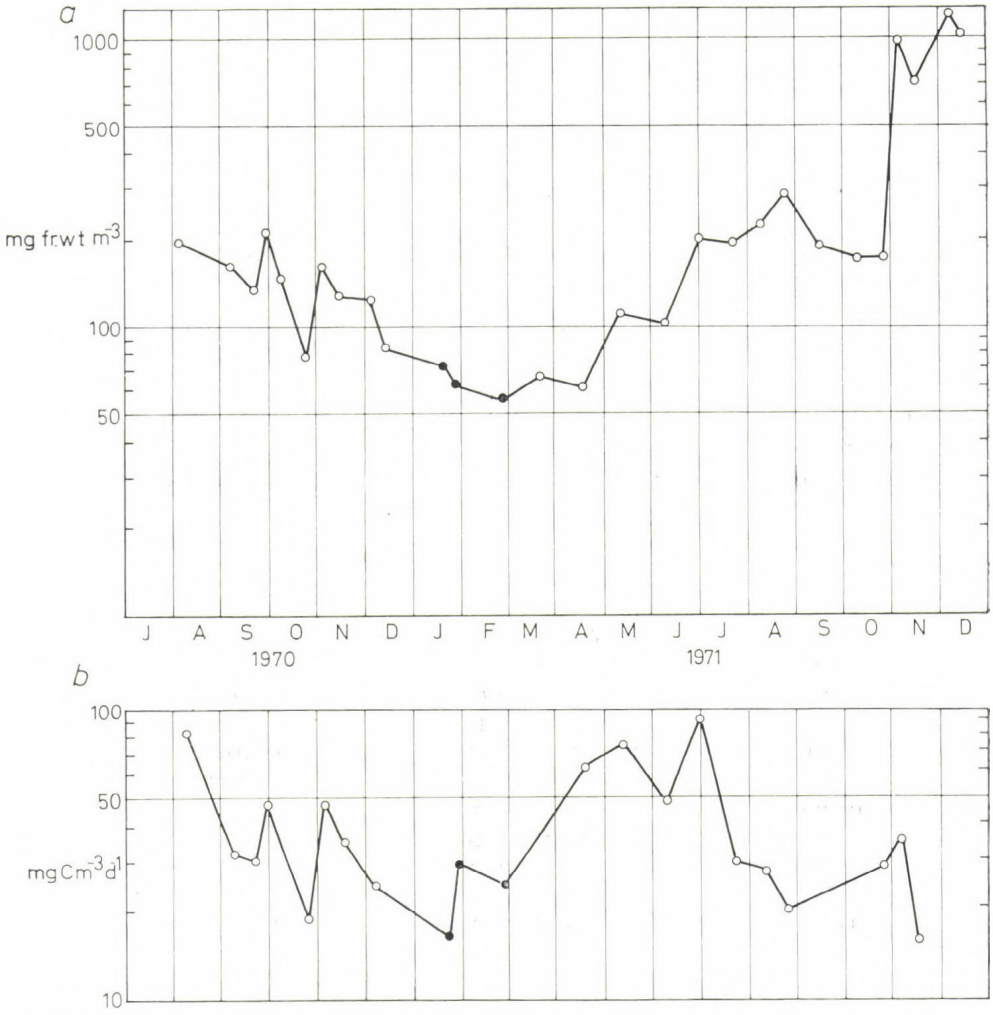


Fig. 1. $1^1/_2$-year cycle of bacterial biomass and production. (*a*) Total bacterial biomass as mg fresh weight per $m^{-3}$. (*b*) Dark carbon uptake in mg C $m^{-3}$, $d^{-1}$. Black circles are values under ice cover

period of ice cover (Fig. 1*a*). Tilzer (1972) has some evidence for a connection between bacterial biomass and inorganic turbidity. Neusiedlersee is an ideal lake for the establishment of such a connection and as it can be seen in Fig. 2, a dependence clearly exists. Winter values seem to be independent of turbidity, but with increasing concentration of inorganic particles bacterial cell counts increase and have a tendency to level off at the highest concentrations. The correlation coefficient of 0.74 is highly significant at the 99 per cent level of confidence. The population increase might be due to bacteria stirred up together with mud particles through wind-generated turbulence. The explanation for the plateau on the right-hand side of the

graph might be the nutrient limitation or a reflection of the total incorporation of the bacteria of the bottom mud into the water column. Saprophytic bacteria (Fig. 3) rapidly increasing after ice break reach their maximum value around August with a subsequent decline till the end of the year. A comparison of Fig. 3 with Fig. 1*a* clearly shows that the highest saprophytic counts do not correspond in time with the total counts. This peak

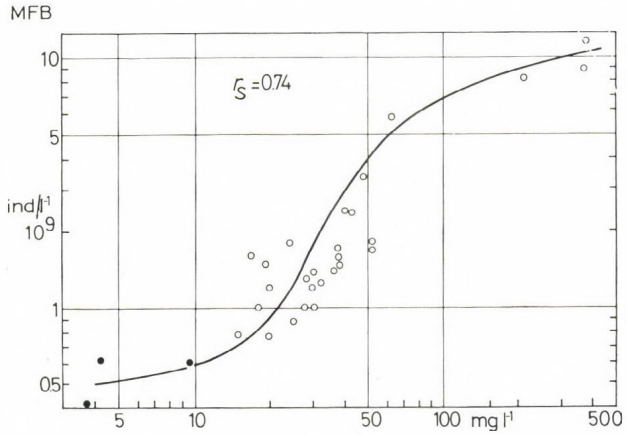


Fig. 2. Correlation of bacterial cell counts on membrane filters (MFB) to inorganic turbidity (T). The curve was fitted by eye and the correlation coefficient calculated. Black circles indicate the period of ice cover

TABLE 1

*Total and viable counts in the sediment*

| Date | MF-bacteria (ind. $10^9$/g fr. wt) | Colony counts (C × $10^3$/g fr. wt) | Dehydrogenase activity (ext./10 g mud) |
|---|---|---|---|
| 4.4.72 | 18.9 | 509 | 0.044 |
| 25.5.72 | 20.4 | 168 | 0.016 |
| 7.6.72 | 21.5 | 168 | 0.018 |
| 22.6.72 | 17.4 | 147 | 0.016 |
| 23.8.72 | 24.5 | 216 | 0.028 |

of heterotrophic bacteria could be due to some breakdown of macrophytes which increase the concentration of dissolved organic compounds.

A few measurements indicate that both total and saprophytic bacteria are higher by a factor of 1,000 in the sediment (Table 1) compared to the concentration in the water column.

## *Production*

Carbon uptake in the dark was taken as a measure of bacterial production (Kusnetsov and Romanenko 1966). The reliability of these values was proved by the change-in-number method (Gak et al. 1972) converted to cell

carbon, according to Troitsky and Sorokin (1967). The converted values are approx. 10 per cent higher than the measured carbon uptake. Therefore, it seems unnecessary to use the formula of Romanenko (1963) for production calculation from $^{14}C$-data (see also discussion of heterotrophic carbon uptake in Tilzer 1972). Daily rates were calculated by multiplying the hourly rate

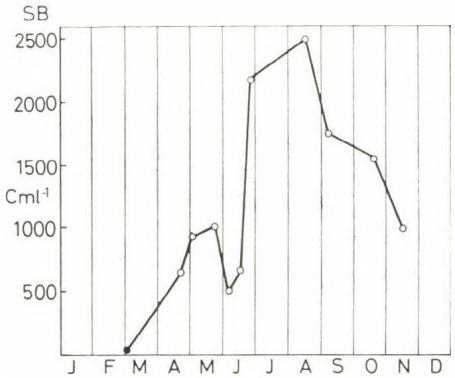


Fig. 3. Heterotrophic saprophytic bacteria (SB) on plates (1971)

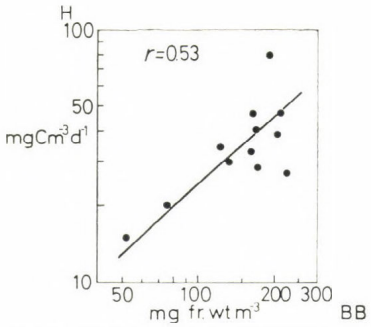


Fig. 4. Correlation of bacterial biomass (BB) and dark carbon uptake (H)

TABLE 2

*Daily cycle of dark carbon uptake from cumulative 2-hour experiments compared with calculated figures by multiplying the hourly rate by 24*

| 6–8 | 8–10 | 10–12 | 12–14 | 14–16 | 16–18 | 18–6 | Sum |
|---|---|---|---|---|---|---|---|
| 1.2 | 2.72 | 1.38 | 3.04 | 2.04 | 2.38 | 12.72 | 25.6 |
| | | | 4.40 | | | | 26.4 |

by 24. This is possible because the observation of Tilzer (1972), that there is a decrease in carbon uptake during the day, is not valid for Neusiedlersee (Table 2).

Heterotrophic carbon uptake is relatively well correlated with total bacterial biomass (Fig. 4).

The unexpectedly high uptake rate relative to the total biomass is puzzling. It was proved that no radioactive carbon is adsorbed on the inorganic particles. The amount of carbon taken up by algae in the dark should be established by using the method of Takahashi et al. (1970), but it is probable that this amount is small.

Figure 1*a* and *b* shows good agreement between production and biomass throughout the year. Values are, in general, low in winter under the ice cover and high in the second period of the year. Production per unit biomass varies between 0.3 and 8.3.

Heterotrophic uptake (H) is independent of photosynthetic carbon uptake (A) under ice but highly correlated during the rest of the year (Fig. 5).

From this graph it can be concluded, as Tilzer (1972) points out, that excretion of organic compounds by algae is the most important factor controlling heterotrophic production.

Calculating the rate of heterotrophic to autotrophic carbon uptake (Fig. 6) one finds that bacterial production exceeds primary production by a factor of 10 in winter under the ice. The rate decreases after ice break until the end of June possibly due to a lack of soluble organic compounds. In July, a rapid increase up to 0.55 : 1 leads to a more or less stable rate. This increase corresponds with a breakdown of the zooplankton population (Herzig 1974).

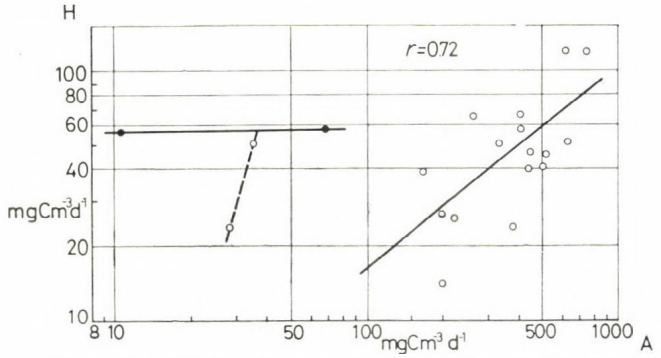


Fig. 5. Correlation of heterotrophic carbon uptake (H) to photosynthetic uptake (A), both in mg C $m^{-3}$ $d^{-1}$ for 1970. Black circles: ice cover


Fig. 6. Annual cycle of the relation of heterotrophic (H) to photosynthetic (A) C-uptake for 1970. Relation under ice is indicated by triangles

*Destruction*

Some preliminary measurements of destruction rates revealed relatively slow decomposition in the sediment and a somewhat higher turnover in the water column. More investigations on destruction in mud and water and on benthic bacteria should be carried out before the end of IBP.

*

*Acknowledgements.* I wish to thank Prof. Dr. J. Overbeck and Doz. Dr. M. Tilzer for their helpful introduction to the methods of freshwater microbiology.

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*Symp. Biol. Hung.*, *15*, pp. 141–147 (1975)

# DESTRUCTION OF ORGANIC MATTER IN THE WATER OF SOME MASURIAN LAKES OF VARYING TROPHISM

by

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All organic matter produced either by plants in autotrophic processes of photosynthesis or by animals in heterotrophic processes, and all allochthonous organic matter entering freshwaters, is decomposed and then mineralized. In these processes being directly or indirectly related to the productivity of aquatic ecosystems and organisms of different trophic level bacteria play the most important role.

In aquatic ecosystems heterotrophic bacteria predominate, their contribution to the number of bacteria exceeding 90 per cent. It should be, however, remembered that not only the number of bacteria is essential to characterize ecosystems and their biological, physical and chemical properties, but also the activity of bacteria, their ability to transform organic matter.

From the chemical point of view two stages of decomposition can be distinguished: (1) hydrolysis processes resulting in the breakdown of complex organic compounds to more simple low-molecular weight compounds and (2) oxidation processes of simple compounds with such final mineral compounds being produced as $CO_2$ (carbon dioxide), $H_2S$ (hydrogen sulphide), $NH_4$ (ammonium), $-PO_4$ (phosphates) and other simple compounds used by bacteria and phytoplankton. Both these stages are due to the action of microorganisms. The enzymes occurring in bacterial cells being responsible for basic processes of living cells take part in the decomposition of organic matter and so do adaptive enzymes produced only in the presence of specific substrates.

Organic matter of the aquatic ecosystems is not uniform, but it represents a multicomponent system containing readily decomposable simple compounds as well as highly complex compounds not readily hydrolysable as e.g. cellulose, lignin, chitin and other substrates, let alone highly polymerized structures entering freshwaters via industrial wastes. The decomposition processes of such a chemically diversified organic matter are determined by the dominant types of macro- and microorganisms being present in the multispecies community.

This report has aimed at presenting the results of the study on the utilization rate of different kinds of organic matter by heterotrophic bacteria in lakes of different trophic type.

The studied lakes are situated in the north-east of Poland, in the Masurian Lake District. These are the mesotrophic Lake Mamry and eutrophic lakes Tałtowisko, Sniardwy, Mikołajskie, Bełdany, Nidzkie and Guzianka.

The utilization rate of the following substrates was studied: glucose, sucrose, salicin, amylose, cellobiose, cellulose, being utilized by bacteria as

a source of carbon, and also asparagine and bactopepton used as a source of carbon and organic nitrogen. In addition, multicomponent substrates were studied in the form of natural organic matter being obtained from the water of a eutrophic lake by freezing, as well as by drying and powdering cells of zoo- and phytoplankton and the reed *Phragmites communis*. All these substrates occur in natural lakes being the products of macrophytic and phytoplanktonic photosynthesis. They are added to the lake water at the rate of 10 mg per litre.

The method of choice in the study was based on measuring the amounts of oxygen used by natural bacterial populations inhabiting the lakes, after elimination of zoo- and phytoplankton, and after a 24–48-hour period of incubation in the dark at a standard temperature of 19–20 °C. The $A/B$ index of heterotrophic activity of bacterial microflora was calculated where $A$ was the amount of oxygen used by bacteria (mg per litre) from the water samples with the added substrate and $B$ was the amount of oxygen (mg per litre) used by bacteria under the same conditions and within the same time, from the water samples without substrate (control samples) (Godlewska-Lipowa 1974*a–d*). The amount of oxygen was measured by Winkler's method.

The studied lakes form a trophic gradient. The increase in eutrophy was followed by an increase in the number of bacteria ranging from $2.0 \times 10^6$/ml in the mesotrophic Lake Mamry to 15.0 or $20 \times 10^6$/ml of water in the most eutrophicated Lake Guzianka (Fig. 1, curve 1). The increase in the number

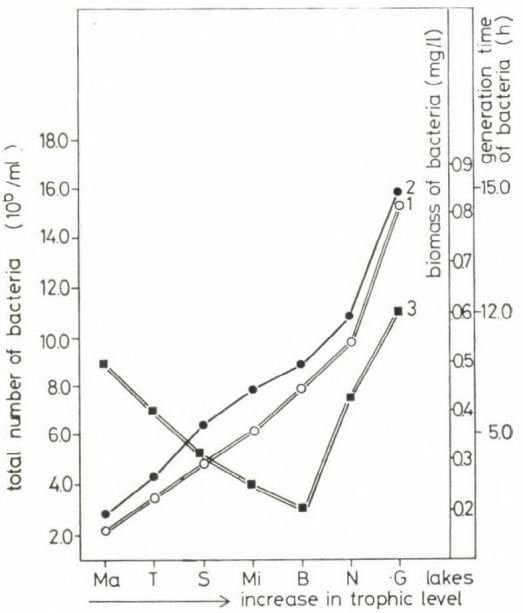


Fig. 1. Total number of bacteria ($10^6$/ml) (curve 1), biomass of bacteria (mg/l) (curve 2) and the generation time of bacteria (h) (curve 3) in Masurian lakes with different trophic levels (Ma = Mamry, T = Tałtowisko, S = Sniardwy, Mi = Mikołajskie, B = Bełdany, N = Nidzkie, G = Guzianka)

of bacteria regarded here as one of the criteria of the degree of eutrophication was accompanied by an increase in bacterial biomass (Fig. 1, curve 2).

The generation time of multispecies microbial communities in natural lake water also depends, to some extent, on the trophic state (Godlewska-Lipowa 1969, 1970). The rate of bacterial cell division (at the logarithmic phase of the bacterial population growth rate) is slightly lower in mesotrophic lakes than in eutrophic ones, and the increase in the eutrophication of the lakes is followed by a decrease in the rate of bacterial cell division (Fig. 1, curve 3).

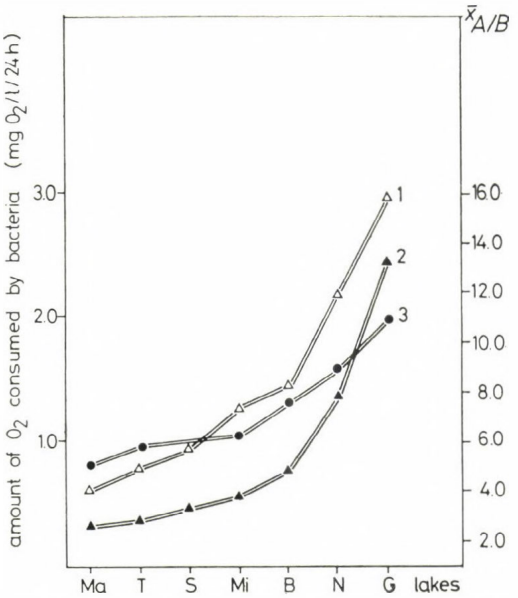


Fig. 2. Amount of $O_2$ consumed by bacteria ($mgO_2$/l/24h) (curve 1), and coefficient of the activity of heterotrophic bacteria ($A/B$) calculated for glucose (curve 2) and bactopepton (curve 3), in Masurian lakes of different trophic levels (for legends see Fig. 1)

The study of the endogenous respiration of bacteria in natural lake water without added substrates indicates that there is a significant relationship between the amount of oxygen used and eutrophication (Fig. 2, curve 1). The lowest endogenous respiration of bacteria was found in the mesotrophic lake, and the highest rate was recorded in the most eutrophicated lake. This regularity does not concern, however, saprobiotic lakes highly polluted with industrial wastes and sewage (this problem will not be discussed here in detail, although it has partly been elaborated).

The activity index of heterotrophic bacterial microflora characterizes, to a great degree, the rate of organic matter decomposition in lakes. It has been calculated for all lakes in question at different depths from epilimnion to hypolimnion.

The obtained results were used to calculate average values characterizing the studied ecosystems. The activity indices were calculated for all substrates

mentioned above. It has been found that some of them tend to increase with an increase in eutrophication.

The average values of the heterotrophic activity index calculated for glucose and bactopepton (Fig. 2, curves 2 and 3) increase in proportion to the increase in the number and biomass of bacteria and in the endogenous respiration rate and thus, proportionally to eutrophication. Glucose and bactopepton are substrates commonly used by the majority of heterotrophic bacteria dominating the aquatic ecosystems. That is why the relationship between the number of bacteria and the activity index calculated for these substrates is so significant. The lowest values of the total heterotrophic activity index (glucose) were found for the mesotrophic Lake Mamry and the highest ones for Lake Guzianka. Intermediate values were found for other lakes.

Sucrose is a disaccharide utilized in lakes by bacteria at different rates (Fig. 3, curve 1). A significant increase was observed in the utilization of this substrate with an increase in the number of bacteria: a marked decrease in the activity index was recorded in polytrophic Lake Bełdany and Lake Nidzkie, which is polluted with cellulose sewages: an increase was observed in Lake Guzianka.

Salicin is a glucoside assimilated probably only by some physiological groups of bacteria (Fig. 3, curve 2). It is a product of terrestrial and perhaps aquatic macrophyte photosynthesis. It is dissolved and passes as a substrate from the land into lakes. A slight but apparent increase was found in salicin utilization by bacteria with an increase in eutrophication. The lowest values

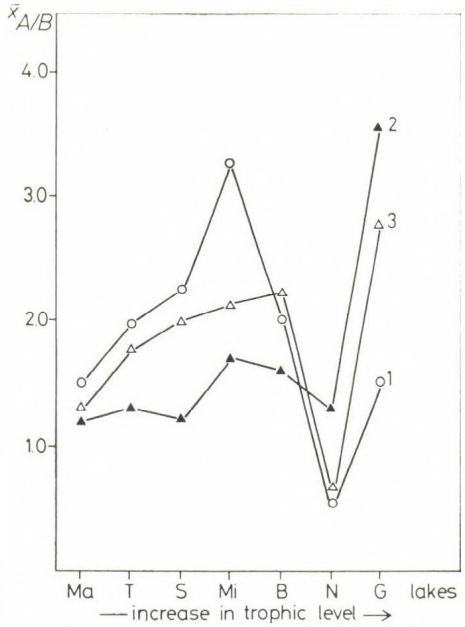


Fig. 3. Coefficient of the activity of heterotrophic bacteria ($A/B$) calculated for sucrose (curve 1), salicin (curve 2) and asparagine (curve 3) in Masurian lakes of different trophic level (for legends see Fig. 1)

were found for the mesotrophic Lake Mamry and the highest ones for Lake Guzianka. The inhibition of bacterial activity in relation to this substrate could be observed in Lake Nidzkie; the activity index was considerably lower than in eutrophic lakes.

A similar curve of the activity index was found for asparagine (Fig. 3, curve 3). Its utilization rate considerably increased with the increase in eutrophication. As in the case of salicin and sucrose, a definite inhibition of bacterial activity was observed in relation to asparagine for Lake Nidzkie.

Cellobiose is a substance slightly more resistant to decomposition than those discussed above. As a product of cellulose hydrolysis it is utilized only by some groups of bacteria. The activity indices were low (Fig. 4, curve 1) and tended to increase with the increase in trophic level.

Attention should be payed to the cellulolytic activity index of the microbial community calculated for cellulose (Fig. 4, curve 2). Cellulose is used by special physiological groups of bacteria producing cellulase. It is a substrate very resistant to chemical hydrolysis; it can be degraded only by adaptive enzymes of the cellulase type. Cellulolytic bacteria do not represent a uniform group from the point of view of systematics, and owing to the presence of cellulase they are a physiologically specific group. Cellulolytic activity was low in all the studied lakes except for Lake Nidzkie where the recorded values of the activity index several times exceeded those found for other lakes. This lake was polluted with sewage from cellulose and hardboard-works; at present it is contaminated by the sewage and

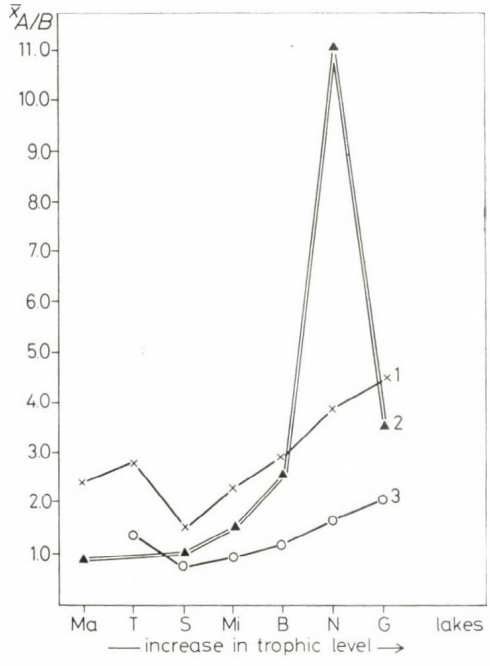


Fig. 4. Coefficient of the activity of heterotrophic bacteria ($A/B$) calculated for cellobiose (curve 1), cellulose (curve 2) and amylose (curve 3) in Masurian lakes with different trophic levels (for legends see Fig. 1)

wastes from a sawmill. The high values of the cellulolytic activity index indicate that the lake is highly polluted. In this case the cellulolytic activity index may be regarded as a diagnostic test. It seems that, because of pollution, infavourable physicochemical conditions have been created for the development of bacterial groups requiring other metabolic substrates. Consequently, there is a significant inhibition in the utilization of the abovementioned substrates including also readily assimilable asparagine.

Amylose is also one of the substrates not readily hydrolysable. It is used by amylolytic bacteria producing amylase (Fig. 4, curve 3). The activity index of amylolytic bacteria is not high in the studied lakes, it increases, however, with an increase in eutrophication. Polysaccharides of the type of amylose and cellulose are the products of phytoplanktonic and macrophytic photosynthesis; this seems to be the reason why the indices of amylolytic and cellulolytic activity increase with an increase in trophic level. These indices can also be considered, to some extent, ones characterizing the primary production of organic matter, being the basic criteria of lake classification.

Multicomponent substrates are highly resistant to bacterial decomposition, and the indices found for three studied complexes were low. The organic matter obtained by freezing lake water is more readily decomposed in highly eutrophic lakes than in the those of low eutrophy (Fig. 5, curve 1); the same can be said about zoo- and phytoplankton cells containing protein and lipid complexes, pieces of cellulose or chitin and also other compounds in the form of organic silicates (Fig. 5, curve 2). The reed *Phragmites*

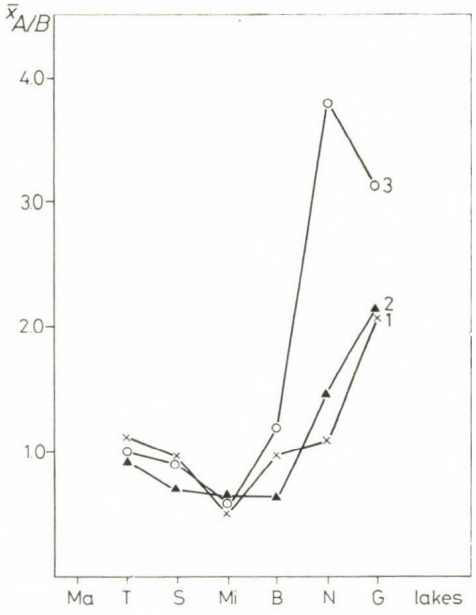


Fig. 5. Coefficient of the activity of heterotrophic bacteria ($A/B$) calculated for polycompound organic matter (curve 1), zoo- and phytoplankton (curve 2) and *Phragmites communis* (curve 3) in Masurian lakes with different trophic levels (for legends see Fig. 1)

*communis* is most ntensively decomposed in Lake Nidzkie. In addition to cellulose, it certainly contains large amounts of lignin (Fig. 5, curve 3). Its decomposition in this lake seems to be justified, due to the presence of sewage and wastes from a sawmill located at this lake. Thus the bacterial microflora degrading this type of chemical structures is abundant there.

The obtained results indicate that there is a close relationship between the decomposition rate of organic matter expressed in the form of an index of heterotrophic microbial activity, and the eutrophication of the lakes. The results of microbiological analysis have allowed the assessment of some parameters characterizing the eutrophication of the lakes. These are as follows: total number and biomass of bacteria, generation time of bacteria and also the heterotrophic activity index characterizing the rate of decomposition of organic matter in lakes.

So far the criteria of lake classification have been based on parameters characterizing production of organic matter. In addition to production processes, those of organic matter decomposition occur in the lakes. Besides production, they constitute a basic element of ecosystem productivity, joining particular links of the trophic web. A knowledge of the dynamics of these processes at different stages in the ecosystems of different trophic types will enable us to get an insight into the mechanisms and functioning of this ecosystem as well as to assess some general regularities controlling them. This is the way of creating new ecological environments.

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*Symp. Biol. Hung.*, *15*, pp. 149–155 (1975)

# METALIMNION FUNCTION IN SHALLOW LAKES

by

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In the ecosystems of deep, stratified eutrophic lakes the main function of the metalimnion is fulfilled by the isolation of sediment and its extension, i.e. the anoxic, nutrient-rich hypolimnetic water from the epilimnion having a high rate of metabolism with a limited nutrient supply. Due to this function the autochthonous nutrient replenishment in the epilimnion is largely restricted to the vernal and autumnal overturn.

Investigating the deep, stratified eutrophic Kolksee (Schleswig-Holstein; Oláh et al. 1973) and a number of shallow Hungarian lakes, a clear, functional analogy has been found between the metalimnion of the stratified Kolksee and the oxidized sediment surface of shallow lakes. The qualitative comparison of several physicochemical profiles in the deep Kolksee and the shallow Lake Balaton demonstrates this analogy (Fig. 1). In deep lakes there is a temperature-density gradient in the metalimnion besides the presence of oxygen to isolate the nutrient-rich anoxic hypolimnetic water. In case of shallow lakes the disappearance of oxidized sediment surface merely induces an upwelling of nutrient-rich anoxic interstitial water. The presence or absence of oxidized sediment surface, i.e. the availability of oxygen at the sediment-water interface is one of the most important factors affecting the structure and functioning of shallow lake ecosystems.

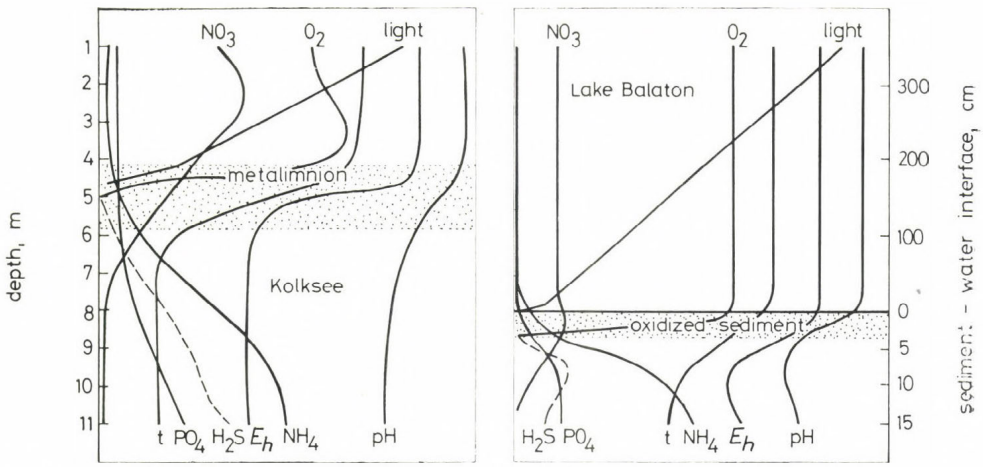


Fig. 1. Qualitative comparison of physicochemical profiles in the deep Kolksee and the shallow Lake Balaton. t = temperature, $E_h$ = redox potential

Using the Milkbrink microstratification sampler we have determined the redox profile of the sediment-water interface in a number of shallow Hungarian lakes (Fig. 2). The extent of the oxidized sediment zone was negatively correlated with the organic load, community respiration and reducing power of the sediment as well as with the lenitic nature of the lake or that of the bottom water (Fig. 3). Significant temporal changes have been detected in the redox profiles both of a highly loaded sewage oxidation pond and in those of Lake Balaton. The thickness of the visible oxidized sediment surface in Lake Balaton was less than 1 cm but only in summer after a long calm period and after the spring flood of River Zala in the highly

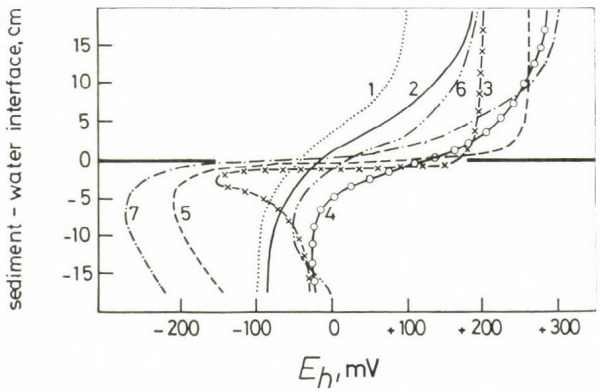


Fig. 2. Redox profiles at the sediment-water interface of shallow lakes. 1, Lake Velence, Cladophora-covered bottom; 2, Lake Velence, reeds-sheltered area; 3, Lake Velence, open water; 4, Lake Balaton, less productive area; 5, Lake Balaton, highly productive area; 6, Lake Belső; 7, Sewage oxidation pond

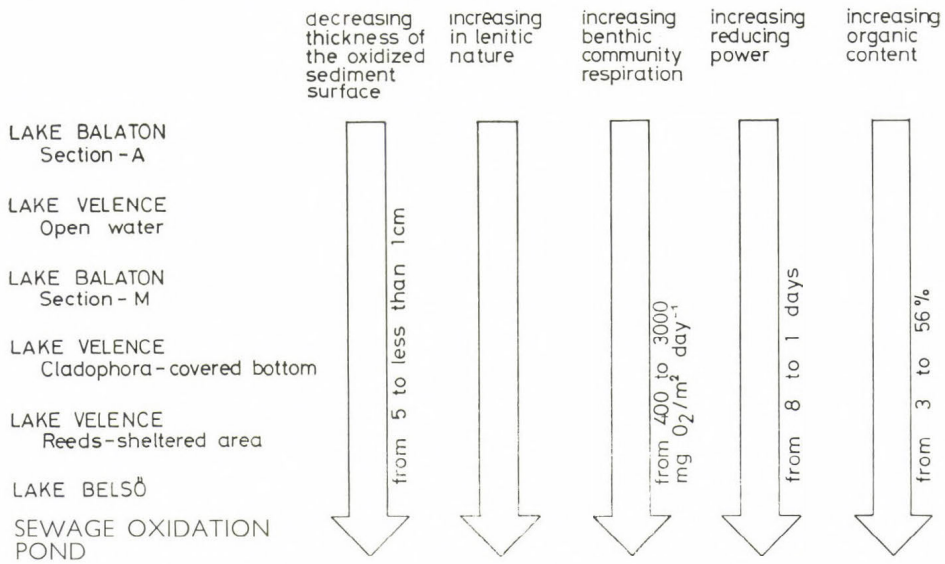


Fig. 3. Relation of the thickness of oxidized sediment zone to benthic parameters

productive Keszthely-Bay. The under-ice redox profiles in Lake Balaton are characterized by a thick oxidized sediment surface due to the significant epibenthic algal production of oxygen induced by appropriate light condition (Herodek and Oláh 1973). In a highly loaded sewage oxidation pond we have measured a diel periodicity in the vertical movement of the reduced sediment zone. During the larger part of the day, the sediment surface was oxidized having an $E_h$ value of +300 mV. The reduced sediment zone rose

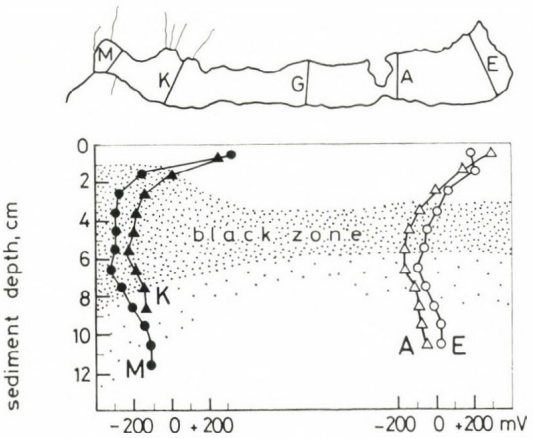


Fig. 4. Territorial differences in the redox profile and the thickness of the oxidized sediment zone in Lake Balaton

to the sediment surface for a short time just before sunrise with an $E_h$ value of +10 mV. This diel movement of the reduced zone seems to have an important role in maintaining the permanent summer bloom of blue-green algae in this sewage oxidation pond. In the large shallow Lake Balaton there are significant territorial differences in the thickness of the oxidized sediment surface (Fig. 4). The visual thickness was measured on glass tube cores, according to the position of the blackish zone. This iron-sulphide-containing zone appeared usually after the fall of $E_h$ below the value of 0 mV. The oxidized upper layer was thinnest in the highly productive Keszthely-Bay and in the adjacent areas receiving the majority of the inflowing waters with high organic load.

The thickness of the oxidized sediment surface in shallow lakes depends primarily on the oxygen balance of the whole ecosystem. To demonstrate this dependence we have investigated the daily oxygen budget of Lake Balaton in the less productive area of section A and in the highly productive area of section M (Table 1). In both parts of the lake the photosynthetic oxygen production exceeds the sum of planktonic and benthic oxygen consumption. Owing to this positive oxygen balance, we could measure a considerable accumulation of oxygen even in the water of the ice-covered lake (Herodek and Oláh 1973). Nevertheless, at the prevailing trophic state in Keszthely-Bay with this very high total oxygen consumption, there is a real chance for the development of a negative oxygen balance at least in the bottom water layers. Under appropriate environmental

TABLE 1

*Daily oxygen budget*
(mg $O_2/m^2$ $day^{-1}$)

| | Lake Balaton | |
|---|---|---|
| | Less productive area 12 July, 1973 | Highly productive area 14 June, 1973 |
| Photosynthetic oxygen production ($P$) | 1,820 | 9,400 |
| Planktonic oxygen consumption | 840 | 5,625 |
| Benthic oxygen consumption | 648 | 2,040 |
| Total consumption ($R$) | 1,488 | 7,665 |
| $P$–$R$ | 332 | 1,735 |

conditions (long calm weather, high water temperature), the oxygen deficit in the bottom water leads to the total disappearance of the constantly thin, oxidized sediment surface.

At the reduced sediment-water interface, a significant amount of organic and inorganic nutrients dissolved in the anoxic interstitial water enters the water column and serves as a nutrient supply further increasing the trophic level of the lake. This is a particular feedback mechanism operating at higher trophic levels of shallow lakes. At present, this mechanism cannot occur in the less productive larger part of Lake Balaton owing to the thick oxidized sediment surface maintained by the positive oxygen balance, but does operate periodically in the highly productive Keszthely-Bay and operates daily in the investigated sewage oxidation pond which has a diel periodicity in the vertical movement of the reduced sediment zone. The reduced sediment-water interface especially promotes the development of blue-green algal blooms (Oláh 1971). The function of the disappearance of the oxidized sediment surface lies also in the decreased decomposition rate of organic materials, besides the nutrient enrichment of the water column. In the less productive part of Lake Balaton with a thick oxidized sediment surface, the decomposition of available organic matter is very rapid accounting for the extremely low summer minima of both total and heterotrophic bacterioplankton. At the same time, in the Keszthely-Bay with a periodically occurring reduced sediment surface, the decomposition rate can slow down resulting in very high summer maxima of the total and heterotrophic bacterioplankton.

The quantitative aspects of the mechanisms involved in the nutrient-enriching and decomposition-retarding effect of the reduced sediment-water interface have not been thoroughly studied. During the recent years, several quantitative studies have been made on phosphate release from reduced sediment of different lakes (Burns and Ross 1971, Björk et al. 1972, Tessenow 1972). The dissolved $PO_4$-P concentration in the water of Lake Balaton is very low, 1–3 $\mu$g per l, and there has been no detectable change during the last fourty years (Oláh et al. in prep.) at least in the larger, less productive part of the lake. This steady state concentration of dissolved inorganic phosphate in the water of this lake is maintained by the chemical nature of the water and the constant disturbance of the oxidized

sediment surface. The adsorption isotherms of $PO_4$-P, both in the less productive area and in the highly productive Keszthely-Bay, indicate a very high adsorption capacity of the oxidized sediment in this lake (Fig. 5). The high, dissolved inorganic phosphate content of inflowing waters including also domestic sewages is rapidly precipitated and adsorbed by the sediment. This process explains the relatively high total-P content even in the open water sediment of the less productive area (0.05 per cent).

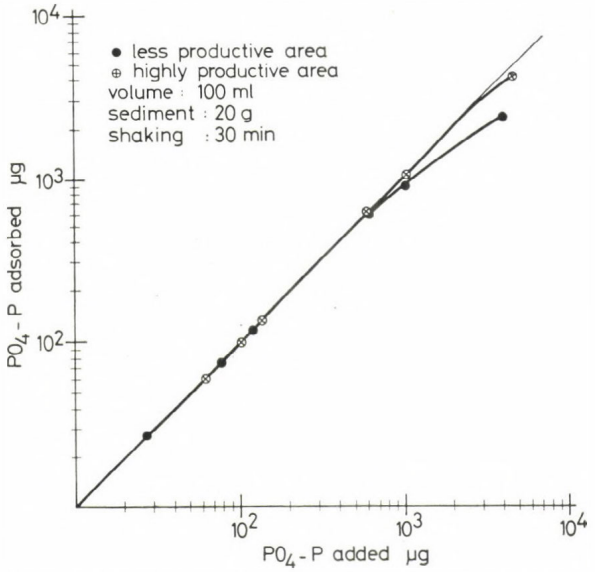


Fig. 5. Adsorption isotherms of $PO_4$-P adsorbed by fresh lake sediment

At the reduced state of the sediment surface this inactivated phosphate may be rapidly released into the water through the iron sulphur–phosphorus system or at a more acid anaerobic pH profile through the calcium carbonate–phosphorus system. In Lake Balaton, the pH range of the reduced sediment-water interface is more acid than that of the oxidized sediment-water interface and promotes the $PO_4$-P release through a calcium carbonate–phosphorus system (Fig. 6). Under anaerobic experimental conditions, the daily release of $PO_4$-P from the sediment of Lake Balaton, especially in the highly productive Keszthely-Bay, is significant but lower than in eutrophic stratified lakes, or in the highly polluted shallow lakes (Fig. 7). The cumulative release is linear up to the 94th day of incubation in the case of the less productive area, and to the 25th day of incubation at the sediment-water interface of Keszthely-Bay (Fig. 8).

In the greatest part of the lake the photosynthetic organic production is moderately low and seasonally constant (Herodek and Tamás 1973) including even the winter, under ice production (Herodek and Oláh 1973). This seasonally constant primary production may duly be explained by the steady-state nature of inorganic phosphate pool available for direct utilization. This steady state was destroyed slowly in Keszthely-Bay due to the increased input of organic and inorganic nutrients resulting, at the same

time, in a slow increase of organic production to a critical level just enough to induce the establishment of a periodically occurring reduced sediment surface. This sediment surface releases a significant amount of phosphate to supply a higher level of primary production which results, simultaneously,

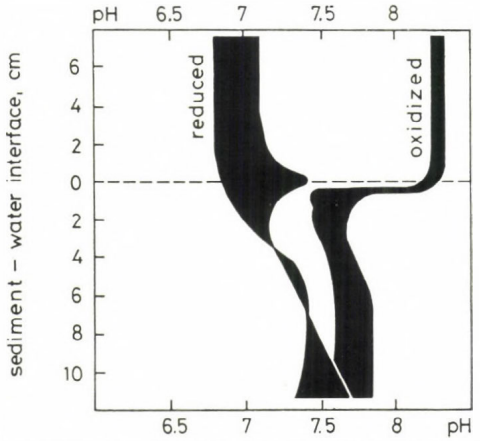


Fig. 6. pH range of the oxidized and reduced sediment-water interface of Lake Balaton

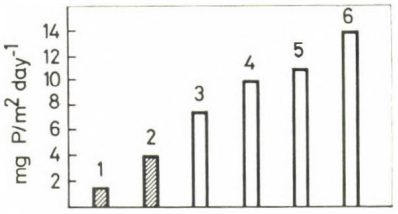


Fig. 7. Release of $PO_4$-P (or total P) from the reduced sediment in different lakes. 1, Lake Balaton, less productive area; 2, Lake Balaton, highly productive area; 3, Lake Erie; 4, Linsley-Pond; 5, Ursee; 6, Lake Trummen

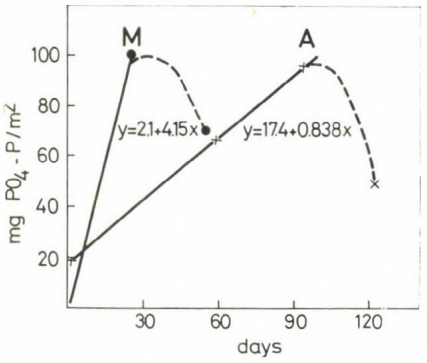


Fig. 8. Cumulative release of $PO_4$-P from the sediment of Lake Balaton under anaerobic experimental conditions. M = highly productive area; A = less productive area

in increased periods of reduced sediment surface, releasing more phosphate and further increasing the organic production within the system (Fig. 9). The outcome is a self-accelerated eutrophication in shallow lakes—reaching this critical level of organic production or allochthonous organic load—through the positive runaway feedback mechanism of anaerobic phosphate release.

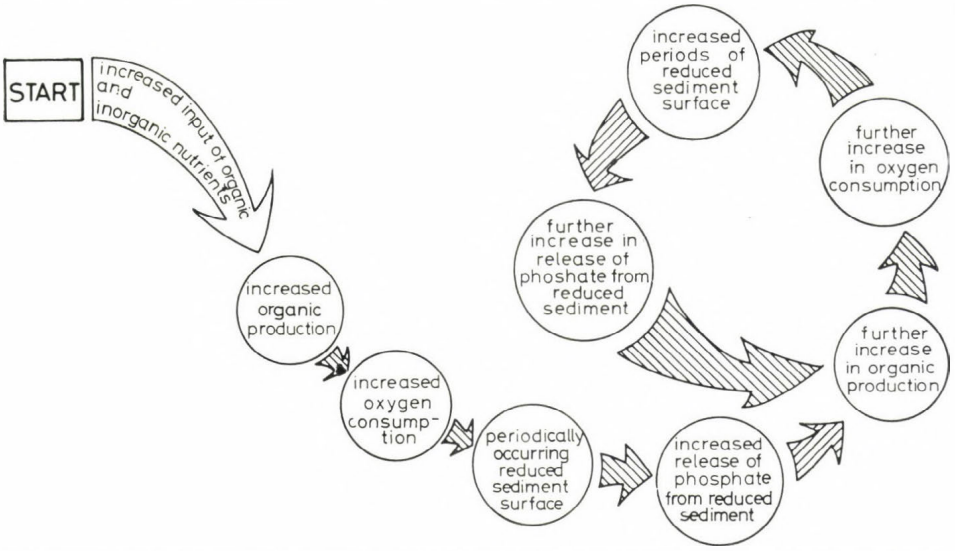


Fig. 9. Self-accelerated eutrophication through positive feedback mechanism of anaerobic phosphate release

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*Symp. Biol. Hung.*, *15*, pp. 157–165 (1975)

# THE IMPORTANCE OF TOTAL AND MIXED-LAYER DEPTH IN THE SUPPLY OF ORGANIC MATERIAL TO BOTTOM COMMUNITIES*

by

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## INTRODUCTION

When a quantity of organic matter is produced in or added to a shallow well-mixed water column, it may be equally available for consumption by pelagic or benthic organisms. Similar additions to a deep or stratified water column, however, may be almost entirely consumed or decomposed by pelagic communities with a very small fraction reaching the bottom. Planktonic and benthic communities thus compete for a common supply of organic matter and the proportion obtained by bottom organisms may be inversely related to water column depth, or if stratification occurs, to the mixed-layer or thermocline depth.

Larkin (1964), in his review of Rawson's studies on Canadian lakes, suggests that increased depth of mixing may result in greater decomposition in the euphotic zone with a corresponding decrease in supply of organic matter to the bottom. He noted that in four large northern Canadian lakes, the ratio of plankton to bottom fauna standing crop was least in well-mixed Lake Winnipeg and greatest in deeper stratified lakes. Although a similar relationship could not be shown for twelve Saskatchewan lakes, Larkin's observations do show that in some cases the size of planktonic and benthic communities may be inversely related in a depth-dependent fashion.

Recent investigations have demonstrated that production by organisms in pelagic and benthic communities may be linked. Hall et al. (1970) measured zooplankton and benthos production in a series of shallow ponds under various conditions of nutrient enrichment and fish predation. While biomass and production varied with treatment, the ratio of zooplankton : benthos production remained close to unity over a three-year period. Rowe (1971) quantified the decrease in benthic biomass with increasing depth in various oceanic areas and concluded that, while depth was of predominant importance, differences in animal biomass were also directly related to differences in phytoplankton primary production. Jónasson (1972) also observed the importance of products of primary production for the growth of *Chironomus* in Lake Esrom profundal sediments. Biomass increments were greatest during periods of spring and autumn overturn, presumably due to mixing and the supply of freshly produced organic matter from surface waters.

A different approach which also allows production processes in surface waters to be related to energy input to sediment communities is demonstrat-

* Bedford Institute of Oceanography Contribution.

ed by Ohle's (1956, 1962) comparison of primary production and sedimentation in some North German lakes. Mineralization was greatest in surface layers, an observation supported by Ławacz's (1969) measures of energy and organic content of sedimenting material in Lake Mikołajki. Ohle (1956) also suggested, however, that the efficiency of mineralization was directly related to mean depth (surface area : volume) in different lakes and that residual organic matter in sediments may be proportional to a measure of ecosystem productivity, 'total potential energy of a lake', expressed on a volume basis.

Few attempts have been made to use chemical measures in sediments as indices of aquatic ecosystem productivity (Hayes 1964, Rybak 1969). Concentrations of total organic matter and organic carbon and nitrogen at the sediment surface have been shown to change seasonally as a result of sedimentation (Kleerekoper 1953, Rybak 1969) but no quantitative relations between standing measures and rates of flux of such organic materials across a sediment interface have been established. The present study compares sedimentation, organic carbon supply, mixing depth and surface sediment organic content in different aquatic ecosystems. The comparisons quantify the importance of water column mixing depth in determining the proportion of carbon supply which reaches the bottom in certain aquatic ecosystems and they demonstrate that surface sediment organic matter in these areas depends in part on the rate of supply of organic material through sedimentation.

## METHODS

### *Carbon supply*

Primary production by phytoplankton, and in some cases by littoral macrophyte communities, is the major carbon source in all areas considered here. Calculated total annual carbon supply also includes estimates of allochthonous organic matter or sewage input where these additions occur. Both light-dark bottle oxygen and $^{14}C$ techniques have been used to measure net phytoplankton photosynthesis in various areas. Macrophyte production has been measured in similar ways or by various harvesting methods. No attempt has been made to discriminate between these measures on the basis of technique, although it is realized that estimates of production may be different when determined by alternate methods. Comparisons of carbon supply in different areas can be made, however, if errors in individual estimates are small relative to the range of measurements compared. Values for annual carbon supply range from 50 to 800 g C $m^{-2}$ for areas compared here and thus errors in individual estimates will probably not alter any general conclusions.

### *Sedimentation*

Comparison of sedimentation rates estimated in different areas is also difficult. Johnson and Brinkhurst (1971) showed that variously shaped collecting vessels catch different amounts of sediment; their data indicate an inverse relation between trap diameter and sedimentation rate. When traps

with large tube openings or funnels are used turbulence may result in resuspension and thus low sedimentation rates are calculated. Bottom material resuspended during periods of water column turbulences will also be measured as sedimentation, but this does not represent a new source of organic material for the sediment surface. Also, no matter what the shape of the collecting vessel, both horizontally and vertically moving particles are trapped. Comparison is justified, however, on a relative basis if it is assumed that material caught in sediment traps is potentially available to sediments at the sampling depth. Sedimentation is expressed as organic carbon which is assumed to be 50 per cent of the organic weight of sedimenting material if direct measures were not made.

### *Sediment organic matter*

In all studies summarized here measures of sediment organic matter have been determined either by loss in weight on ashing at 550 °C for 1 to 3 hours, or by direct analysis of carbon using an elemental analyser and conversion to organic weight by a factor of 0.50. Ashing procedures may dehydrate clays and in some studies (Wetzel et al. 1972) this was corrected by treating ashed sediment with distilled water and redrying before determination of ash-free dry weight.

## RESULTS

A step-wise multiple linear regression was used to examine the data in Table 1 and to quantify correlations between total depth, mixed-layer depth, carbon supply and sedimentation (Table 2). Carbon supply was directly related to sedimentation and accounted for 55 per cent of the variance while mixed-layer depth was inversely related and accounted for an additional 24 per cent of the variance. Sedimentation was not significantly related to total water column depth. Logarithmic transformation of variables increased the amount of variance attributable to mixed-layer depth to 38 per cent in which case 93 per cent of the variance (total $mr^2$) in sedimentation was accounted for by differences in carbon supply and mixing depth.

Since logarithmic transformations only slightly altered the regression calculations, linear relations between the variables may be assumed and sedimentation can be directly related to carbon supply and inversely related to mixed-layer depth. The inverse relation with mixing depth is clearly demonstrated when sedimentation is expressed as a percentage of supply (Fig. 1). This comparison standardizes different rates of sedimentation in various areas by correcting for differences in carbon supply. Also, since both mixed-layer depth and carbon supply are independently related to sedimentation, the ratio of carbon supply : mixed-layer depth can be used to compare sedimentation directly to supply and inversely to mixed-layer depth on a single graph (Fig. 2). A linear regression provided the best fit to the data.

Several studies of sedimentation have included measurements of organic matter in bottom sediments at depths corresponding to sediment trap

collections (Table 3). Surface sediment organic content is linearly related to the logarithm of annual sedimentation in these different areas (Fig. 3).

If turbulence does not add or remove significant amounts of material relative to that sedimenting, an index of mineralization of sedimented material may be derived by comparing the organic content of sedimenting substances with that found at the sediment surface. The smallest changes in

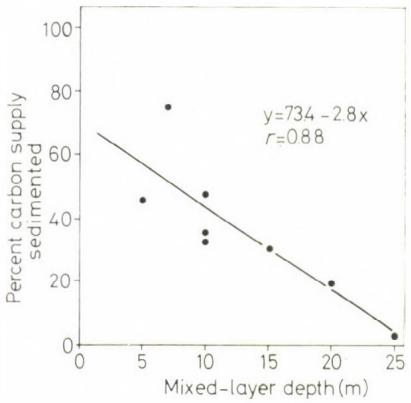


Fig. 1. Comparison of annual estimates of organic carbon sedimentation, expressed as a percentage of supply, and mixed-layer (thermocline) depth during stratification. Data taken from various areas summarized in Table 1

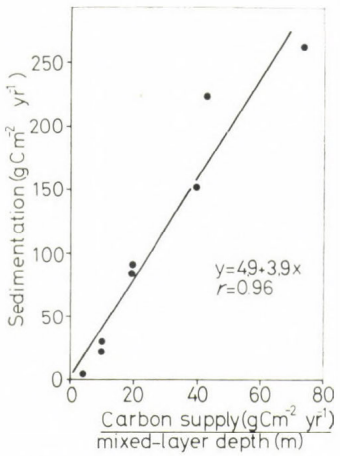


Fig. 2. Organic carbon sedimentation expressed as a linear function of the ratio of carbon supply : mixed-layer depth. Data from different areas taken from Table 1

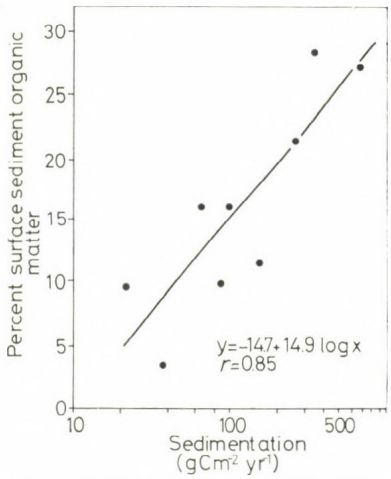


Fig. 3. Comparison of the logarithm of annual organic carbon sedimentation and average per cent organic matter in surface sediment at the collection depth. Data taken from various areas summarized in Table 3

TABLE 1

*Comparison of annual estimates of carbon supply and sedimentation in various areas with different total and mixed-layer depths*

| Location | Depth (m) | | g C $m^{-2}$ $yr^{-1}$ | | Per cent supply sedimented |
|---|---|---|---|---|---|
| | Total | Mixed-layer | Supply | Sedimentation | |
| 1. St. Margaret's Bay | 65 | 20 | 792[a] | 153[b] | 19 |
| 2. Lake Mikołajki | 24 | 10 | 730[c] | 262[d] | 36 |
| 3. Departure Bay | 30 | 7 | 300[e] | 225[e] | 75 |
| 4. Bedford Basin | 60 | 15 | 280[f] | 87 | 31 |
| 5. Lake Esrom | 18 | 10 | 191[g] | 92[h] | 48 |
| 6. Lake Biwa | 50 | 25 | 99[i] | 3[i] | 3 |
| 7. Lawrence Lake | 12 | 5 | 48[j] | 22[j] | 46 |
| 8. Loch Ewe | 25 | 10 | 90[k] | 30[k] | 33 |

*References and comments:*

[a] Platt (1971*a*), Mann (1972), total supply taken as sum of phytoplankton and littoral seaweed production.
[b] M. Paranjape (Unpublished).
[c] Kajak et al. (1972).
[d] Ławacz (1969).
[e] Stephens et al. (1967), assumes 100 g C $m^{-2}$ $yr^{-1}$ allochthonous input.
[f] Platt and Irwin (1971*b*), estimated sewage input added to measured primary production (230 g C $m^{-2}$ $yr^{-1}$).
[g] Jónasson (1972).
[h] E. Hansen (Unpublished).
[i] Toyoda et al. (1968), assumed C : N = 42 : 7.
[j] Wetzel et al. (1972), measured carbon supply taken from pelagic carbon budget omitting resuspension and estimates of bacterial chemosynthesis and heterotrophy.
[k] Steele and Baird (1972).

TABLE 2

*Results of a step-wise multiple linear regression of data in Table 1. Annual carbon supply* ($X_1$) *and mixed-layer (thermocline) depth* ($X_2$) *compared with annual sedimentation* ($Y$)

| | Correlation matrix | | |
|---|---|---|---|
| | $X_1$ | $X_2$ | $Y$ |
| $X_1$ | 1 | 0.155 | 0.742 |
| $X_2$ | 0.155 | 1 | — 0.336 |
| $Y$ | 0.742 | — 0.336 | 1 |

| Iteration no. | Slope coefficient | | S.D. | T-ratio | $mr^2$ |
|---|---|---|---|---|---|
| 1 | constant | 120.6 | | | |
| 2 | constant | 35.2 | | | |
| | $X_1$ | 0.245 | 0.099 | 2.47 | 0.55 |
| 3 | constant | 108.9 | | | |
| | $X_1$ | 0.268 | 0.082 | 3.27 | |
| | $X_2$ | −6.24 | 3.35 | −1.86 | 0.79 |

sediment organic content occur in the two areas (Lake Windermere and Big Bay) with the highest sedimentation rates where terrestrial debris accounts for a large fraction of the organic input (Table 3). If these areas are excluded, there is a trend towards decreasing loss of organic matter

TABLE 3

*Comparison of annual estimates of sedimentation and surface sediment organic content in various areas*

| Location* | Sedimenting material | | g C $m^{-2} yr^{-1}$ | Surface sediment per cent organic matter | Per cent organic matter lost after sedimentation |
|---|---|---|---|---|---|
| | Collection depth (m) | Per cent organic matter | | | |
| 1. Bedford Basin | 60 | 15.4 | 87 | 9.8 | 5.6 |
| 2. St. Margaret's Bay | 65 | 18.3 | 153 | 11.4 | 6.9 |
| 3. Lake Mikołajki | 24 | 40.0 | 262 | 21.5 | 18.5 |
| 4. Lake Ontario | 30 | 32.0 | 38 | 3.5 | 28.5 |
| 5. Bay of Quinte | | | | | |
| *a*) Conway | 35 | 26.0 | 66 | 16.0 | 10.0 |
| *b*) Glenora | 20 | 28.0 | 77 | 16.0 | 12.0 |
| *c*) Big Bay | 4 | 34.0 | 348 | 28.0 | 6.0 |
| 6. Lake Windermere (N) | 60 | 30.0 | 688 | 27.0 | 3.0 |
| 7. Lawrence Lake | 11 | 20.0 | 22 | 9.5 | 10.3 |

* *References and comments:*

1, 2 – results from unpublished studies in progress.
3 – Ławacz (1969) and Rybak (1969).
4, 5 – Johnson and Brinkhurst (1971).
6 – Tutin (1955) measured sedimentation as 2.6 mm per yr. Specific gravity assumed as 1.8 in calculating total weight sedimented.
7 – Wetzel et al. (1972).

after sedimentation with increasing depth. Thus, where sediments originate largely from products of autochthonous primary production, the greatest changes in organic content after sedimentation occur in shallow water.

## DISCUSSION

It has been 17 years since Ohle (1956) demonstrated that production and decomposition processes in euphotic surface waters may be closely linked with only a small fraction of the carbon supply actually sedimenting. His suggestion that the amount of organic material incorporated into sediments is inversely related to depth and directly proportional to organic carbon concentration in overlying water has never been examined. Thomas (1955) did not measure production in his study of an oligotrophic and two eutrophic German lakes which were characterized on the basis of their nutrient and oxygen levels. He suggested, however, that since sedimentation was greater in the euphotic lakes this could be used as an index of production. Since these early studies there have been numerous investigations of production, sedimentation and decomposition at sediment surfaces, but except for the recent study by Wetzel et al. (1972), it has not been possible to compare all three processes in one area.

The importance of morphometry, usually expressed as mean depth (volume : surface area), in determining the relative importance of pelagic and benthic communities in lakes has long been known (Thienemann 1927; Rawson 1961). There is no comparable measure to mean depth in marine areas since, except for enclosed bays, surface area is not restricted. However,

there is generally a positive correlation between water body size (surface area) and both total and mixed-layer depth. Thus, mixing depth, measured as thermocline depth during stratification, may be roughly comparable to estimates of mean depth.

The inverse relation between sedimentation and mixing depth (Fig. 1) may in part reflect wind-induced circulation which resuspends bottom sediments. Gorham (1958) suggested that turbulent displacement determined the thickness of oxidized surface lake muds and Davis (1973) has observed resuspension of 6–12 mm of sediment in littoral areas of a dimictic lake. Such mixing may occur only at lake overturn or, as in Lake Suwa, it may occur throughout the year and result in a direct correlation between wind velocity and sedimentation (Koidsumi and Sakurai 1968). Larkin (1964) has also noted that as lake size increases, the proportion of area occupied by the littoral zone decreases. Thus, possible resuspension of material from these areas, as well as the addition of allochthonous matter from shores, may decrease in importance as a source of sedimenting material as water body size and mixing depth increase.

Carbon supply and sedimentation in various areas are directly related ($r = 0.74$) although because of the limited data the regression is not significant ($p < 0.05$, Table 2). The unusually high proportion of carbon supply sedimented in Departure Bay may reflect the importance of terrestrial runoff in this area. One-third of the total carbon input occurs between October and December when runoff is maximum. The high inorganic content and a C : N ratio of 10 : 1 indicate an allochthonous supply and profiles of suspended material during this period show rapid deposition (Stephens et al. 1967). Products of phytogenous origin do not sediment as rapidly, however, and there may be considerable delay between peaks in primary production and sedimentation.

No constant relationship between timing of peak periods of supply and sedimentation appears to exist for various areas considered here. In some cases, such as Departure Bay, there is a two-month lag between the spring phytoplankton bloom and increased phytodetritus in sediments. In Lake Mikołajki, on the other hand, while maximum primary production occurs during August, the greatest energy input to sediments occurs during May and November (Kajak et al. 1972, Rybak 1969). Some factors which would delay sedimentation have been discussed by Stephens et al. (1967) and among these the stability of the water column, with associated changes in vertical mixing rates, would appear to be most important.

The relation between the ratio of carbon supply : mixed-layer depth and sedimentation (Fig. 2) supports my previous observation (Hargrave 1973) that this ratio may serve to index the input of organic material to bottom communities. The relationship appears to adequately describe data from both freshwater and marine areas. The shape of the curve, however, may largely depend on the source of the data. Data from oceanic areas are lacking for the comparison but low annual rates of primary production (50 to 100 g C $m^{-2}$ $yr^{-1}$) with great mixed-layer depths (25 to 100 m) will produce ratios which would cluster near the origin of Fig. 2. More data are needed from shallowly mixed areas with high levels of carbon supply. This would allow the predictive nature of the relationship to be determined for high levels of sedimentation.

Ohle's (1956) suggestion that residual organic matter in sediments may be used as a measure of water body productivity is supported by the relationship between sedimentation and surface sediment organic matter (Fig. 3). Interpretation of the comparison is made difficult, however, by large seasonal and spatial difference which may occur in surface sediment organic content (Rybak 1969, Wetzel et al. 1972, Hargrave, unpublished data). In many of the areas summarized in Table 3, the greatest discontinuities in sediment organic matter occur at depths which correspond to the extent of mixing during stratification. Presumably water turbulence in shallow littoral areas resuspends sediment material which slowly accumulates in deeper water where less physical transport occurs (see Wetzel et al. 1972).

If processes of sediment re-distribution are common, comparison of organic matter in sedimenting material with that found at a sediment surface must be made cautiously. The problem is avoided to some extent by comparing these measures in different areas and by assuming that material caught in sediment traps reflects what is potentially available to sediments at the collection depth. There is also difficulty in applying these considerations to acidic oligotrophic waters where humic substances produce sediments with high organic content which decompose slowly. Sedimentation in these areas may be low and yet sediment organic matter may be very high, indicative of slow rates of oxidation.

Small changes in organic content after sedimentation in Big Bay and Lake Windermere support the authors' suggestion that sedimenting material is derived, at least in part, from terrestrial sources. Decomposition of such organic material must be very slow and little affected by residence time as indexed by water column depth through which sedimentation occurs. Sediments in other areas summarized in Table 3, however, derive largely from products of phytoplankton or macrophyte production. Decomposition of these more readily oxidized compounds may be related to the duration of sedimentation which in turn, for a stratified water column, would be a direct function of depth. A detailed study to compare rates of vertical eddy diffusion, sedimentation and decomposition of sediment trapped at various depths would quantify these relationships.

*

*Acknowledgements.* Studies of sedimentation in Bedford Basin would not have been possible without the technical help of Mrs. G. Phillips and Mr. W. P. Vass. Mr. E. Hansen and M. Paranjape kindly provided unpublished data on sedimentation in Lake Esrom and St. Margaret's Bay.

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*Symp. Biol. Hung.*, *15*, pp. 167–179 (1975)

# THIRTY-YEAR RESEARCH (1943–1973) ON THE LIMNOLOGY OF LAKE SZELID (SZELIDI-TÓ)

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Lake Szelid is today one of the most important and most frequently visited southern holiday resort centres, lying in the Danube valley near Dunapataj (about 110 km from Budapest) (Luther and Rzóska 1971).

The results of all limnological research up to 1957 were published under the auspices of the Hungarian Academy of Sciences in 1959 (Donászy, Ed. 1959). From 1972 until the present time this area has been increasingly developing in the fields of agriculture, industry and culture.

This paper summarizes a number of results on the lake sediment research and attempts to answer some of the questions arising in connection with the problems of chemical budget. These problems have already been discussed, for example, by the Working Group Chemical Budget on the IBP/UNESCO Symposium held in Reading in 1972.

## INTRODUCTION

In the final phase of the IBP/PF it was necessary to devote more attention to some of the special problems concerning shallow freshwater ecosystems. Prior to the Reading Symposium and the Lunz Meeting, and also at the Reading Symposium, plenary sessions were specially arranged due to these problems peculiar to shallow lakes. It is hoped that the Symposium at Tihany may have contributed to the understanding of these shallow freshwater ecosystems (in addition to other questions).

In view of this it seemed most worth while to choose the Lake Szelid ecosystem as a noteworthy example of shallow Pannonian lakes and to select the data of thirty years of research as a means of illustrating examples of some of the problems of these ecosystems.

This contribution has been based on data obtained from the Department of Hydrobiology, Freshwater Laboratory of the National Institute for Agricultural Quality Testing, Budapest (Collaborators: B. Veszprémi, Mrs. I. Fábry and A. Gyánó).

## BOTTOM SURFACE SEDIMENT RESEARCH IN 1968

In this paper only the results of the first research on 14th September, 1968 will be summarized (Fig. 1). Bottom sediment samples were taken in six areas of the lake, three samples in each: two were taken near the shore and the third in the middle of the lake. In each area water samples were

taken, too: one from the middle of the lake from the surface layer, the second just off the bottom, above the position where the sediment samples were taken.

In each case the sediment sample was black. The samples were subsequently dried and homogenized. Aqueous extracts were prepared using distilled water in a ratio of 1 : 10, according to normal practice in soil analysis. The results of the analysis are contained in Tables 1–6.

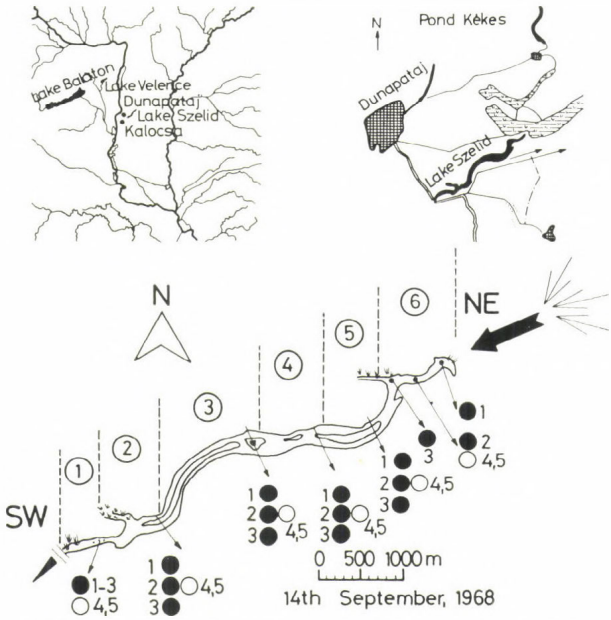


Fig. 1. Map of Lake Szelid. → catchment area; ⇒ inflow; ▶ outflow. Areas No. 1 to 6 have been researched. Full circles: No. of sediment sample; empty circles: No. of water sample

The types of sediments were as follows:

Type 1. Taken from depths of 120, 160 cm at the SW area of the lake. Nature of sediment: gyttja. Colour of aqueous extracts: brownish (odourless).

Type 2. Collected from depths of 150, 250, 280 cm. Nature of the sediment: sand and gyttja. Colour of the aqueous extracts: yellow (odourless). All samples taken in the middle of the lake in areas No. 3 and 4, and near the shore in area No. 4 (depth 150 cm).

Type 3. Taken from depths of 30–40 cm, near the N and S shore line. Nature of sediment: sand. Colour of the aqueous extracts: yellowish. All samples in areas No. 2, 3 and 4 taken near the shore.

Type 4. Taken only in the NE area of the lake (No. 6) from depths of 80, 150 and 200 cm. Nature of sediment: gyttja. Colour of the aqueous extracts: brownish-red (odour of hydrogen sulphide and ammonia). By shaking strong effervescence occurs.

The deepest samples were taken from 350 cm in area No. 2. The nature of the sediment was gyttja, the colour of the aqueous extracts being brownish.

TABLE 1

*Area No. 1 (SW end of Lake Szelid). Chemical analysis of lake sediment and water samples*

(14th September, 1968, see Fig. 1)

| | Lake sediment, aqueous extracts | | | Water samples | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Nature of sediment | gyttja | gyttja | gyttja | — | — |
| Depth in cm | 120 | 120 | 160 | 120 | surface |
| Colour of aqueous extracts | brownish | brownish | brownish | — | — |
| Major elements, mEq/l | | | | | |
| $Ca^{2+}$ | 0.24 | 0.24 | 0.89 | 0.55 | 0.80 |
| $Mg^{2+}$ | 2.96 | 1.36 | 2.31 | 5.50 | 5.25 |
| $Fe^{2+}$ | 0.06 | 0.02 | 0.23 | 0.00 | 0.00 |
| $K^+$ | 0.48 | 0.26 | 0.42 | 0.46 | 0.48 |
| $Na^+$ | 8.26 | 9.57 | 19.57 | 49.59 | 51.33 |
| $Cl^-$ | 1.00 | 1.00 | 13.00 | 28.00 | 27.80 |
| $HCO_3^-$ | 5.10 | 8.16 | 8.16 | 17.95 | 17.95 |
| $CO_3^{2-}$ | 0.00 | 0.00 | 0.00 | 8.56 | 8.56 |
| $SO_4^{2-}$ | 5.09 | 1.61 | 0.84 | 1.52 | 3.49 |
| $PO_4^{3-}$ | 0.06 | 0.09 | 0.13 | 0.01 | 0.01 |
| $SiO_3^{2-}$ | 0.75 | 0.59 | 1.29 | 0.06 | 0.05 |
| Sum of ions, mEq/l | 24.00 | 22.90 | 46.84 | 112.20 | 115.72 |
| Conductivity, $\mu$S | 1,320 | 1,520 | 2,560 | 6,640 | 6,520 |
| pH | 7.37 | 7.35 | 7.45 | 8.65 | 8.70 |
| $NH_4^+$, mg/l | 7.210 | 7.620 | 7.666 | 0.291 | 0.291 |
| (free $NH_3$, pH), $\mu$g/l | (86) | (91) | (107) | (45) | (48) |
| $NO_3^-$, mg/l | 3.532 | 3.532 | 5.176 | 0.329 | 0.415 |
| $NO_2^-$, mg/l | 0.990 | 0.990 | 1.910 | 0.035 | 0.052 |
| $NH_4-N$, $\mu$g/l | 5,624 | 5,944 | 5,975 | 227 | 227 |
| $NO_3-N$, $\mu$g/l | 812 | 812 | 1,191 | 76 | 95 |
| $NO_2-N$, $\mu$g/l | 297 | 297 | 573 | 10 | 16 |
| Sum of anorg. N, $\mu$g/l | 6,733 | 7,053 | 7,739 | 313 | 338 |
| $PO_4$, mg/l | 2.5 | 3.0 | 4.0 | 0.4 | 0.3 |
| $PO_4-P$, $\mu$g/l | 817 | 979 | 1,305 | 132 | 99 |
| $SiO_3$, mg/l | 28.6 | 19.0 | 49.2 | 2.3 | 1.9 |
| $SiO_2-Si$, mg/l | 10.7 | 7.0 | 18.1 | 851 $\mu$g | 703 $\mu$g |
| C.O.D. ($KMnO_4$ in $O_2$), mg/l | 149.44 | 152.95 | 355.13 | 27.70 | 30.34 |

TABLE 2

*Area No. 2 in Lake Szelid. Chemical analysis of lake sediment and water samples* (14th September, 1968; see Fig. 1)

| | Lake sediment, aqueous extracts | | | Water samples | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Nature of sediment | sand | gyttja | sand | — | — |
| Depth in cm | 40 | 350 | 30 | 350 | surface |
| Colour of aqueous extracts | yellowish | brownish | yellowish | — | — |
| Major elements, mEq/l | | | | | |
| $Ca^{2+}$ | 0.24 | 0.32 | 0.32 | 0.80 | 0.80 |
| $Mg^{2+}$ | 0.88 | 2.08 | 0.56 | 4.79 | 4.79 |
| $Fe^{2+}$ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| $K^{+}$ | 0.06 | 0.31 | 0.41 | 0.49 | 0.49 |
| $Na^{+}$ | 3.93 | 21.31 | 3.00 | 52.20 | 51.33 |
| $Cl^{-}$ | 0.22 | 13.20 | 1.50 | 27.80 | 27.60 |
| $HCO_3^{-}$ | 1.84 | 9.18 | 1.22 | 18.15 | 18.35 |
| $CO_3^{2-}$ | 0.00 | 0.00 | 0.00 | 8.97 | 8.97 |
| $SO_4^{2-}$ | 2.72 | 0.77 | 1.42 | 3.29 | 2.42 |
| $PO_4^{3-}$ | 0.05 | 0.14 | 0.05 | 0.01 | 0.01 |
| $SiO_3^{2-}$ | 0.30 | 0.83 | 0.10 | 0.06 | 0.06 |
| Sum of ions, mEq/l | 10.26 | 48.04 | 8.58 | 116.56 | 114.82 |
| Conductivity, $\mu$S | 600 | 2,840 | 544 | 6,520 | 6,520 |
| pH | 7.50 | 7.75 | 7.64 | 8.70 | 8.70 |
| $NH_4^{+}$, mg/l | 1.692 | 13.910 | 2.646 | 0.291 | 0.291 |
| (free $NH_3$, pH), $\mu$g/l | (27) | (334) | (49) | (48) | (48) |
| $NO_3^{-}$, mg/l | 1.240 | 8.203 | 1.716 | 0.415 | 0.346 |
| $NO_2^{-}$, mg/l | 1.053 | 1.189 | 0.402 | 0.051 | 0.008 |
| $NH_4-N$, $\mu$g/l | 1,318 | 10,842 | 1,919 | 227 | 227 |
| $NO_3-N$, $\mu$g/l | 285 | 1,886 | 396 | 95 | 80 |
| $NO_2-N$, $\mu$g/l | 315 | 357 | 121 | 15 | 2 |
| Sum of anorganic N, $\mu$g/l | 1,918 | 13,085 | 2,436 | 337 | 309 |
| $PO_4$, mg/l | 1.7 | 4.5 | 1.7 | 0.4 | 0.4 |
| $PO_4-P$, $\mu$g/l | 555 | 1,468 | 555 | 132 | 132 |
| $SiO_3$, mg/l | 11.6 | 31.7 | 3.8 | 2.2 | 2.2 |
| $SiO_2-Si$, mg/l | 4.4 | 11.8 | 1.5 | 814 $\mu$g/l | 814 $\mu$g/l |
| C.O.D. ($KMnO_4$ in $O_2$), mg/l | 77.35 | 230.31 | 73.84 | 28.69 | 28.51 |

TABLE 3

*Area No. 3 in Lake Szelid. Chemical analysis of lake sediment and water samples*
(14th September, 1968; see Fig. 1)

| | Lake sediment, aqueous extracts | | | Water samples | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Nature of sediment | sand | sand + gyttja | sand | — | — |
| Depth in cm | 30 | 280 | 30 | 280 | surface |
| Colour of aqueous extracts | yellowish | yellow | yellowish | | — |
| Major elements, mEq/l | | | | | |
| $Ca^{2+}$ | 0.24 | 0.89 | 0.41 | 0.80 | 0.80 |
| $Mg^{2+}$ | 0.24 | 3.11 | 0.63 | 4.79 | 4.79 |
| $Fe^{2+}$ | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| $K^+$ | 0.13 | 0.26 | 0.13 | 0.49 | 0.49 |
| $Na^+$ | 2.97 | 5.65 | 3.10 | 52.20 | 52.20 |
| $Cl^-$ | 2.40 | 0.90 | 0.57 | 27.60 | 27.80 |
| $HCO_3^-$ | 0.82 | 5.10 | 1.22 | 18.56 | 18.96 |
| $CO_3^{2+}$ | 0.00 | 0.00 | 0.00 | 8.16 | 8.16 |
| $SO_4^{2-}$ | 0.26 | 3.25 | 2.36 | 3.89 | 3.29 |
| $PO_4^{3-}$ | 0.02 | 0.16 | 0.02 | 0.01 | 0.01 |
| $SiO_3^{2-}$ | 0.08 | 0.50 | 0.10 | 0.06 | 0.06 |
| Sum of ions, mEq/l | 7.16 | 19.82 | 8.54 | 116.56 | 116.56 |
| Conductivity, $\mu$S | 360 | 1,240 | 688 | 6,520 | 6,520 |
| pH | 7.05 | 7.10 | 7.40 | 8.65 | 8.70 |
| $NH_4^+$, mg/l | 1.306 | 12.860 | 1.529 | 0.291 | 0.291 |
| (free $NH_3$, pH), $\mu$g/l | (13) | (129) | (20) | (45) | (48) |
| $NO_3^-$, mg/l | 0.981 | 3.299 | 0.678 | 0.346 | 0.389 |
| $NO_2^-$, mg/l | 0.402 | 0.778 | 0.226 | 0.028 | 0.020 |
| $NH_4-N$, $\mu$g/l | 1,022 | 9,594 | 1,193 | 227 | 227 |
| $NO_3-N$, $\mu$g/l | 226 | 759 | 156 | 80 | 89 |
| $NO_2-N$, $\mu$g/l | 121 | 233 | 68 | 8 | 6 |
| Sum of anorganic N, $\mu$g/l | 1,369 | 10,586 | 1,417 | 315 | 322 |
| $PO_4$, mg/l | 0.8 | 5.0 | 0.6 | 0.4 | 0.3 |
| $PO_4-P$, $\mu$g/l | 261 | 1,632 | 196 | 132 | 99 |
| $SiO_3$, mg/l | 3.2 | 19.0 | 3.7 | 2.2 | 2.2 |
| $SiO_2-Si$, mg/l | 0.8 | 7.0 | 1.4 | 814 $\mu$g | 814 $\mu$g |
| C.O.D. ($KMnO_4$ in $O_2$), mg/l | 63.29 | 156.47 | 107.24 | 28.35 | 28.69 |

TABLE 4

*Area No. 4 of Lake Szelid. Chemical analysis of lake sediment and water samples* (14th September, 1968; see Fig. 1)

| | Lake sediment, aqueous extracts | | | Water samples | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Nature of sediment | sand | sand + gyttja | | — | — |
| Depth in cm | 30 | 250 | 150 | 250 | surface |
| Colour of aqueous extract | yellowish | yellow | yellowish | — | — |
| Major elements, mEq/l | | | | | |
| $Ca^{2+}$ | 0.16 | 0.50 | 0.14 | 0.55 | 0.80 |
| $Mg^{2+}$ | 0.56 | 0.94 | 0.87 | 5.04 | 4.79 |
| $Fe^{2+}$ | 0.00 | 0.02 | 0.05 | 0.00 | 0.00 |
| $K^+$ | 0.13 | 0.26 | 0.13 | 0.49 | 0.46 |
| $Na^+$ | 1.88 | 3.27 | 4.18 | 51.33 | 52.20 |
| $Cl^-$ | 1.18 | 0.42 | 1.94 | 27.80 | 27.80 |
| $HCO_3^-$ | 1.12 | 1.63 | 1.43 | 17.95 | 17.95 |
| $CO_3^{2-}$ | 0.00 | 0.00 | 0.00 | 8.56 | 8.56 |
| $SO_4^{2-}$ | 0.08 | 2.75 | 2.07 | 3.01 | 3.88 |
| $PO_4^{3-}$ | 0.03 | 0.02 | 0.03 | 0.01 | 0.01 |
| $SiO_3^{2-}$ | 0.32 | 0.17 | 0.17 | 0.08 | 0.05 |
| Sum of ions, mEq/l | 5.46 | 9.98 | 11.28 | 114.82 | 116.50 |
| Conductivity, $\mu$S | 440 | 784 | 920 | 6,520 | 6,520 |
| pH | 7.57 | 7.03 | 7.61 | 8.70 | 8.75 |
| $NH_4^+$, mg/l | 1.245 | 1.286 | 1.854 | 0.291 | 0.291 |
| (free $NH_3$, pH), $\mu$g/l | (22) | (13) | (35) | (48) | (52) |
| $NO_3^-$ | 1.197 | 0.981 | 0.332 | 0.346 | 0.389 |
| $NO_2^-$ | 1.358 | 0.255 | 0.304 | 0.017 | 0.017 |
| $NH_4$—N, $\mu$g/l | 967 | 1,006 | 1,443 | 227 | 227 |
| $NH_3$—N, $\mu$g/l | 276 | 226 | 76 | 80 | 89 |
| $NO_2$—N, $\mu$g/l | 408 | 76 | 91 | 5 | 5 |
| Sum of anorganic N, $\mu$g/l | 1,651 | 1,308 | 1,610 | 312 | 321 |
| $PO_4$, mg/l | 0.9 | 0.6 | 1.0 | 0.3 | 0.3 |
| $PO_4$—P, $\mu$g/l | 294 | 196 | 326 | 99 | 99 |
| $SiO_3$, mg/l | 12.4 | 6.7 | 6.3 | 3.0 | 1.9 |
| $SiO_2$—Si, mg/l | 4.6 | 2.5 | 2.3 | 1.111 | 0.703 |
| C.O.D. ($KMnO_4$ in $O_2$), mg/l | 175.81 | 172.29 | 184.60 | 28.85 | 28.85 |

TABLE 5

*Area No. 5 of Lake Szelid. Chemical analysis of lake sediment and water samples*
(14th September, 1968; see Fig. 1)

| | Lake sediment, aqueous extracts | | | Water samples | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Nature of sediment | sand | sand + gyttja | | — | — |
| Depth in cm | 40 | 280 | 150 | 280 | surface |
| Colour of aqueous extracts | yellowish | yellow | yellowish | — | — |
| Major elements, mEq/l | | | | | |
| $Ca^{2+}$ | 0.16 | 1.02 | 0.62 | 0.80 | 0.80 |
| $Mg^{2+}$ | 0.48 | 1.70 | 2.58 | 4.79 | 4.79 |
| $Fe^{2+}$ | 0.02 | 0.02 | 0.00 | 0.00 | 0.00 |
| $K^{+}$ | 0.13 | 0.13 | 0.26 | 0.49 | 0.46 |
| $Na^{+}$ | 4.18 | 5.18 | 6.61 | 49.59 | 51.33 |
| $Cl^{-}$ | 1.60 | 2.52 | 0.80 | 27.00 | 27.80 |
| $HCO_3^{-}$ | 2.75 | 2.04 | 4.08 | 17.95 | 18.35 |
| $CO_4^{2-}$ | 0.00 | 0.00 | 0.00 | 8.16 | 8.16 |
| $SO_4^{2-}$ | 0.21 | 3.43 | 4.55 | 2.49 | 3.01 |
| $PO^{3-}$ | 0.09 | 0.03 | 0.14 | 0.01 | 0.01 |
| $SiO_3^{2-}$ | 0.32 | 0.15 | 0.50 | 0.06 | 0.05 |
| Sum of ions, mEq/l | 9.94 | 16.34 | 20.14 | 111.34 | 114.76 |
| Conductivity, $\mu$S | 648 | 1,240 | 1,360 | 6,520 | 6,520 |
| pH | 8.55 | 7.36 | 7.70 | 8.70 | 8.70 |
| $NH_4^{+}$, mg/l | 1.493 | 3.804 | 4.410 | 0.291 | 0.291 |
| (free $NH_3$, pH), $\mu$g/l | (179) | (46) | (97) | (48) | (48) |
| $NO_3^{-}$, mg/l | 1.586 | 1.586 | 2.105 | 0.389 | 0.389 |
| $NO_2^{-}$, mg/l | 1.288 | 0.340 | 0.806 | 0.011 | 0.011 |
| $NH_4-N$, $\mu$g/l | 1,162 | 2,964 | 3,440 | 227 | 227 |
| $NO_3-N$, $\mu$g/l | 366 | 366 | 485 | 89 | 89 |
| $NO_2-N$, $\mu$g/l | 612 | 102 | 242 | 3 | 3 |
| Sum of anorganic N, $\mu$g/l | 2,140 | 3,432 | 4,167 | 319 | 319 |
| $PO_4$, mg/l | 3.00 | 1.00 | 4.5 | 0.4 | 0.3 |
| $PO_4-P$, $\mu$g/l | 979 | 326 | 1,468 | 132 | 99 |
| $SiO_3$, mg/l | 12.1 | 5.7 | 19.0 | 2.2 | 1.9 |
| $SiO_2-Si$, $\mu$g/l | 4,500 | 2,100 | 7,000 | 814 | 703 |
| C.O.D. ($KMnO_4$ in $O_2$), mg/l | 158.23 | 161.74 | 114.27 | 28.85 | 28.19 |

TABLE 6

*Area No. 6 (NE) of Lake Szelid. Chemical analysis of lake sediment and water samples* (14th September, 1968; see Fig. 1)

| | Lake sediment, aqueous extracts | | | Water samples | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Nature of sediment | gyttja | gyttja | gyttja | — | — |
| Depth in cm | 80 | 150 | 200 | 150 | — |
| Colour of aqueous extracts | Odour and by shaking strong effervescence | | | | |
| | red-brown | red-brown | red-brown | — | — |
| Major elements, mEq/l | | | | | |
| $Ca^{2+}$ | 0.24 | 0.32 | 0.24 | 0.80 | 0.80 |
| $Mg^{2+}$ | 2.96 | 4.48 | 4.56 | 4.79 | 4.79 |
| $Fe^{2+}$ | 0.15 | 0.06 | 0.06 | 0.00 | 0.00 |
| $K^{+}$ | 0.36 | 0.36 | 0.31 | 0.49 | 0.46 |
| $Na^{+}$ | 13.70 | 15.31 | 15.23 | 51.33 | 51.33 |
| $Cl^{-}$ | 9.60 | 9.80 | 9.80 | 27.80 | 27.80 |
| $HCO_3^{-}$ | 6.12 | 9.18 | 9.18 | 18.35 | 18.35 |
| $CO_3^{2-}$ | 0.00 | 0.00 | 0.00 | 8.16 | 8.16 |
| $SO_4^{2-}$ | 0.56 | 0.33 | 0.34 | 3.03 | 2.99 |
| $PO_4^{3-}$ | 0.13 | 0.09 | 0.08 | 0.01 | 0.01 |
| $SiO_3^{2-}$ | 1.00 | 1.13 | 1.00 | 0.06 | 0.07 |
| Sum of ions, mEq/l | 34.82 | 41.06 | 40.80 | 114.82 | 114.76 |
| Conductivity, $\mu$S | 2,400 | 2,520 | 2,480 | 6,480 | 6,480 |
| pH | 8.00 | 8.10 | 8.10 | 8.70 | 8.70 |
| $NH^{+}$, mg/l | 9.400 | 10.620 | 9.040 | 0.291 | 0.291 |
| (free $NH_3$, pH), $\mu$g/l | (376) | (531) | (452) | (48) | (48) |
| $NO_3^{-}$, mg/l | 3.332 | 4.830 | 3.792 | 0.476 | 0.294 |
| $NO_2^{-}$, mg/l | 1.189 | 1.189 | 0.141 | 0.011 | 0.017 |
| $NH_4$—N, $\mu$g/l | 7,332 | 8,268 | 7,051 | 227 | 227 |
| $NO_3$—N, $\mu$g/l | 765 | 1,111 | 872 | 109 | 68 |
| $NO_2$—N, $\mu$g/l | 357 | 357 | 042 | 3 | 5 |
| Sum of anorganic N, $\mu$g/l | 8,454 | 9,736 | 8,965 | 399 | 300 |
| $PO_4$, mg/l | 4.0 | 3.0 | 2.5 | 0.4 | 0.4 |
| $PO_4$—P, $\mu$g/l | 1,305 | 979 | 917 | 132 | 132 |
| $SiO_3$, mg/l | 38.1 | 42.9 | 38.1 | 2.4 | 2.5 |
| $SiO_2$—Si, mg/l | 14.1 | 15.9 | 14.1 | 888 $\mu$g | 925 $\mu$g |
| C.O.D. ($KMnO_4$ in $O_2$), mg/l | 170.53 | 254.92 | 242.61 | 28.69 | 28.85 |

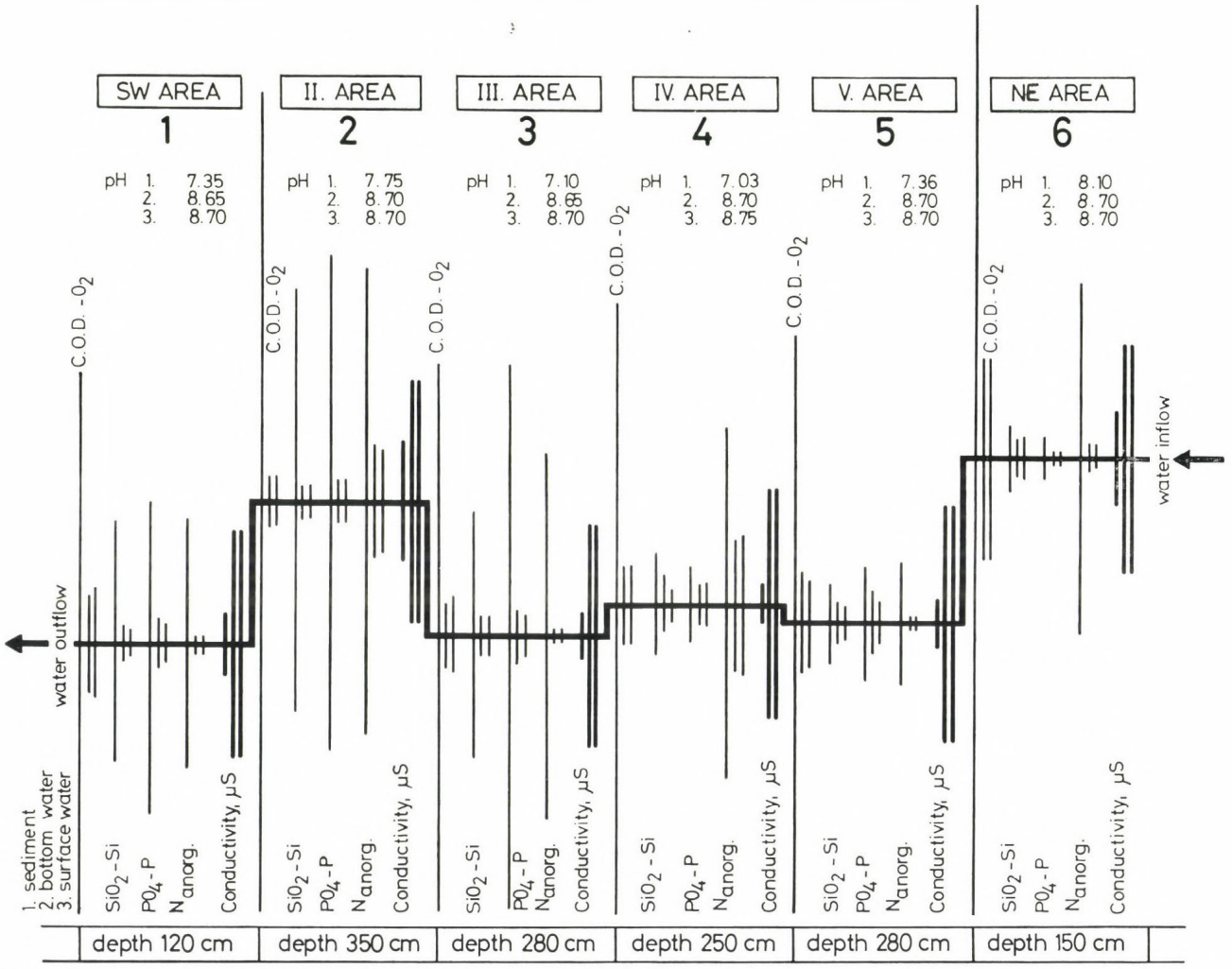


Fig. 2. Nutrient elements of lake sediment and the bottom and surface water of Lake Szelid (14th September 1968). For detailed data see Tables 1 to 6

TABLE 7

*Sulphate reduction in Lake Szelid. Possible mineralization of the lake sediment* (14th September,

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| | $SO_4^{2-}$ mg | $H^+$ mg | Sum mg | kcal cal | S mg | $O_2$ mg | $H_2O$ mg |
| 1 | 3.8 | 0.08 | 3.88 | 5.8 | 1.27 | 1.90 | 0.71 |
| 2 | 10.1 | 0.21 | 10.31 | 15.5 | 3.37 | 5.05 | 1.89 |
| 3 | 12.5 | 0.26 | 12.76 | 19.1 | 4.17 | 6.25 | 2.34 |
| 4 | 15.8 | 0.33 | 16.13 | 24.2 | 5.27 | 7.90 | 2.96 |
| 5 | 16.3 | 0.34 | 16.64 | 29.9 | 5.43 | 8.15 | 3.06 |
| 6 | 26.9 | 0.57 | 27.46 | 41.2 | 8.97 | 13.45 | 5.04 |
| 7 | 37.0 | 0.78 | 37.78 | 56.6 | 12.34 | 18.50 | 6.94 |
| 8 | 40.3 | 0.85 | 41.15 | 61.7 | 13.44 | 20.15 | 7.56 |
| 9 | 68.2 | 1.43 | 69.63 | 104.4 | 22.74 | 34.10 | 12.79 |
| 10 | 77.3 | 1.62 | 78.92 | 118.3 | 25.67 | 38.65 | 14.60 |
| 11 | 99.4 | 2.09 | 101.49 | 152.1 | 33.11 | 49.70 | 18.68 |
| 12 | 113.3 | 2.38 | 115.68 | 173.3 | 37.78 | 56.65 | 21.25 |
| 13 | 130.6 | 2.79 | 133.35 | 200.0 | 43.56 | 65.30 | 24.49 |
| 14 | 132.1 | 2.77 | 134.87 | 202.0 | 44.05 | 66.05 | 24.77 |
| 15 | 156.1 | 3.28 | 159.38 | 238.8 | 52.06 | 78.05 | 29.27 |
| 16 | 164.7 | 3.46 | 168.16 | 252.0 | 54.93 | 82.35 | 30.88 |
| 17 | 218.5 | 4.58 | 223.08 | 334.4 | 72.81 | 109.3 | 40.97 |
| 18 | 244.5 | 5.13 | 249.63 | 374.2 | 81.58 | 122.2 | 45.85 |

$$\frac{2}{3}\,SO_4^{2-} + \frac{4}{3}\,H^+ \rightleftharpoons \frac{2}{3}\,S + O_2 + \frac{2}{3}\,H_2O \rightleftharpoons$$

98 kcal

$$\underbrace{64.04 + 1.344}_{65.38} \qquad \underbrace{21.37 + 32 + 12.01}_{65.38}$$

## DISCUSSION OF THE RESULTS

The sediment—which is increasing yearly—is different in the NE region of the lake. It is in this region that the inflow of precipitation from the catchment area of the lake occurs. Fish killings occur throughout the winter period and at the end of winter.

The SW area, that of the outflow, is of a completely different nature. Progressing from SW to NE the lake becomes deeper. Areas No. 2–4 are possibly the most beautiful as well as the widest and deepest. The distance from shore to shore is at the widest point 100–150 m, the depth changing from 4 to 5 m.

In connection with the questions discussed by the Working Group Chemical Budget at the IBP/UNESCO Symposium, we make the following points:

1. With regard to sediment being more important in shallow lakes than in deep ones: in shallow lakes such as Lake Szelid there is a very high concentration of nutrient elements in the sediment (C, N, P, S, Si). Thus

*by microorganisms, based on data of aqueous extracts of 18 sediment samples*
1968; after Fogg 1953)

| 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|
| Sum mg | S mg | $H_2O$ mg | Sum mg | kcal cal | $H_2S$ mg | $O_2$ mg | Sum mg |
| 3.88 | 3.8 | 2.14 | 5.94 | 7.5 | 4.04 | 1.90 | 5.94 |
| 10.31 | 10.1 | 5.68 | 15.78 | 19.9 | 10.74 | 5.05 | 15.79 |
| 12.76 | 12.5 | 7.03 | 19.53 | 24.6 | 13.26 | 6.25 | 19.53 |
| 16.13 | 15.8 | 8.89 | 24.69 | 31.1 | 16.79 | 7.90 | 24.69 |
| 16.64 | 16.3 | 9.17 | 25.47 | 32.1 | 17.32 | 8.15 | 25.47 |
| 27.46 | 26.9 | 15.13 | 42.03 | 52.9 | 28.58 | 13.45 | 42.03 |
| 37.78 | 37.0 | 20.82 | 57.82 | 72.8 | 39.32 | 18.50 | 57.82 |
| 41.15 | 40.3 | 22.68 | 62.98 | 79.3 | 42.83 | 20.15 | 63.98 |
| 69.63 | 68.2 | 38.38 | 106.58 | 134 | 72.48 | 34.10 | 106.58 |
| 78.92 | 77.3 | 43.50 | 120.8 | 152 | 82.15 | 38.65 | 120.80 |
| 101.49 | 99.4 | 55.94 | 155.3 | 196 | 105.60 | 49.70 | 155.30 |
| 115.68 | 113.3 | 63.75 | 177.0 | 223 | 120.25 | 56.65 | 177.0 |
| 133.35 | 130.6 | 73.50 | 204.1 | 257 | 139.0 | 65.10 | 204.1 |
| 134.87 | 132.1 | 74.37 | 206.5 | 260 | 140.5 | 66.0 | 206.5 |
| 159.38 | 156.1 | 87.85 | 243.6 | 307 | 165.6 | 78.0 | 243.6 |
| 168.10 | 164.7 | 92.64 | 257.4 | 324 | 175.1 | 82.3 | 257.4 |
| 223.08 | 218.5 | 122.96 | 341.5 | 429 | 232.4 | 109.2 | 341.6 |
| 249.60 | 244.5 | 137.60 | 382.1 | 481 | 260.0 | 122.1 | 382.1 |

$$\rightleftharpoons 2S + 2H_2O \rightleftharpoons 2H_2S + O_2$$

126 kcal

$$\underbrace{64.12 + 36.04}_{100.16} \qquad \underbrace{68.16 + 32}_{100.16}$$

the nature of the sediment is not only more important in shallow lakes than in deep ones, but also in the various areas of the same shallow lake (e.g. NE area, SW area, the shore, the middle of the lake, etc.).

2. The nature of sediment influences the trophic level of the lake. Sediment plays a more important role in the highly eutrophic shallow lakes.

3. Mineralization of algae in strongly eutrophic lakes is caused by bacteria (and some other microorganisms as, e.g. chemolithotrophic, chemosynthetic algae) rather than by the fauna. Lake Szelid is also illustrative of this aspect. The chemical nature of the lake supports more than 300 algal species and the lake itself has a high primary production, but the relatively small number of zooplankton and fish species does not utilize the phytoplankton biomass. The fauna utilizes only a part of algal biomass.

The high values of C.O.D. (in $KMnO_4 - O_2$), the anorganic nitrogen and $PO_4 - P$, $SiO_2 - Si$, $SO_4^{2-}$, and the gyttja support this hypothesis (Fig. 2).

4. The nutrient transport from the hypolimnion towards the epilimnion is not possible because the nutrients are immediately transported by bacteria from the bottom into the lake water. It is therefore understandable why

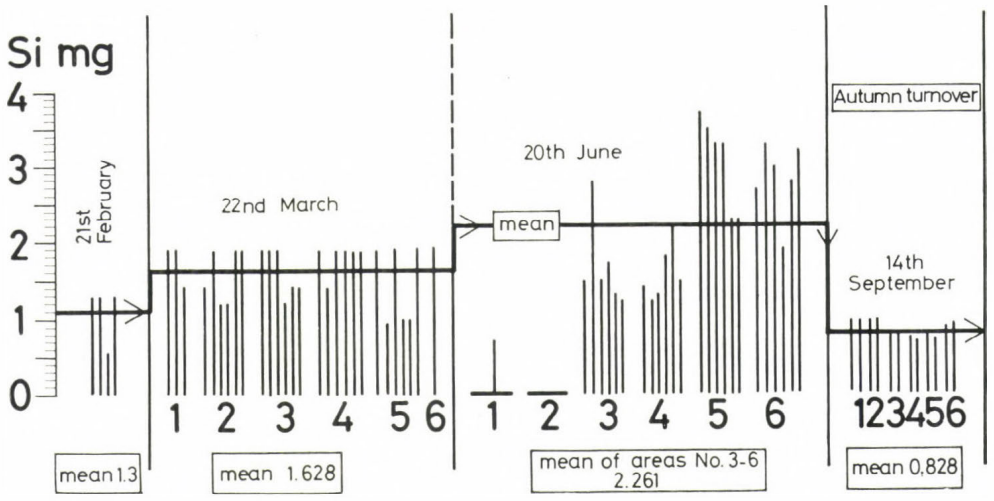


Fig. 3. Molybdate reactive silicate ($SiO_2$–Si) in the water of Lake Szelid (1968). Nos 1–6 = Investigated areas. Six samples were taken in each area except in March and September (only 3 samples in area No. 1 in March). 1. Near the south shore from the surface layer; 2. near the south shore from off the bottom; 3. in the middle of lake from the surface layer; 4. in the middle of lake from bottom layer; 5. near the north shore from the surface layer; 6. near the north shore from the bottom layer. In September in each area two samples were taken, one off the bottom, the other from the surface layer

fish perish so rapidly in winter. The sulphate reduction processes—caused by microorganisms—produce toxic concentration in the lake water (Table 7).

5. In view of our results silicate can be used as a hydrological factor. The Si-analysis in 1968 clearly demonstrated that up to June, the concentration of $SiO_2$—Si increased and from September until the end of winter the values of Si were not high. There are no significant differences in Si-values in the total lake water from bottom to surface layer after the autumn turnover time (Fig. 3).

## SUMMARY

The sediment of Lake Szelid was examined in 1968. Bottom sediment samples were taken from six areas of the lake. Aqueous extracts were prepared and analysed. There were four types of sediment, its nature being different near the shore, in the NE and in the SW area. The nutrient elements are highly concentrated in the gyttja. The nature of the sediment influences the trophic level of the lake. Mineralization of algae in Lake Szelid is caused by bacteria rather than by the fauna. The nutrients are immediately transported by bacteria from the bottom to the water. Silicate can be used as a hydrological factor.

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*Symp. Biol. Hung.*, *15*, pp. 181–187 (1975)

# THE POLLUTION OF THE LAKE AT PALIĆ

by

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## INTRODUCTION

The extent and consequences of pollution are well exemplified by the recent destruction of fish in the lake at Palić (Fig. 1). The problems arose here not only due to a considerable loss of fish, but also to the arrest of water life as a result of pollution following the formation of a general cell-, enzyme- and nerve-poison, i.e. hydrogen sulphide.

According to our present knowledge, there are two ways for hydrogen sulphide to attain concentrations lethal to aquatic living organisms in lakes:

1. It is liberated extremely rapidly as a result of cooling from the large amount of iron sulphide accumulated in the reduction zone of the mud. With the cooling-down, the oxygen content of the water increases, and thus the iron sulphide in the surface mud layer is oxidized to sulphuric acid. In contrast to carbonic acid, this strong mineral acid is capable of liberating hydrogen sulphide from the residual iron sulphide (Vámos 1964, 1968).
2. Another means of attaining high hydrogen sulphide concentration is when there is no available iron either in the mud or the water, and consequently hydrogen sulphide cannot be bound as a biologically innocuous iron sulphide. In such a case, a large quantity of molecular hydrogen sulphide accumulates in the mud.


Fig. 1. Geographical situation of the lake at Palić

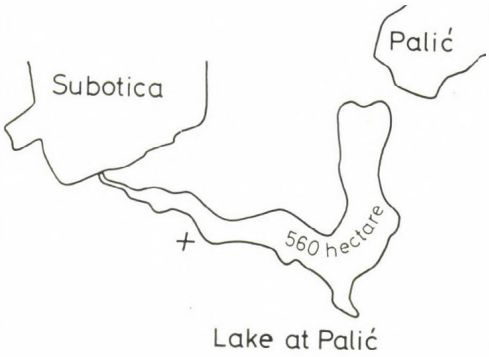


Fig. 2. The lake at Palić: + denotes the site where the first dead fish were observed

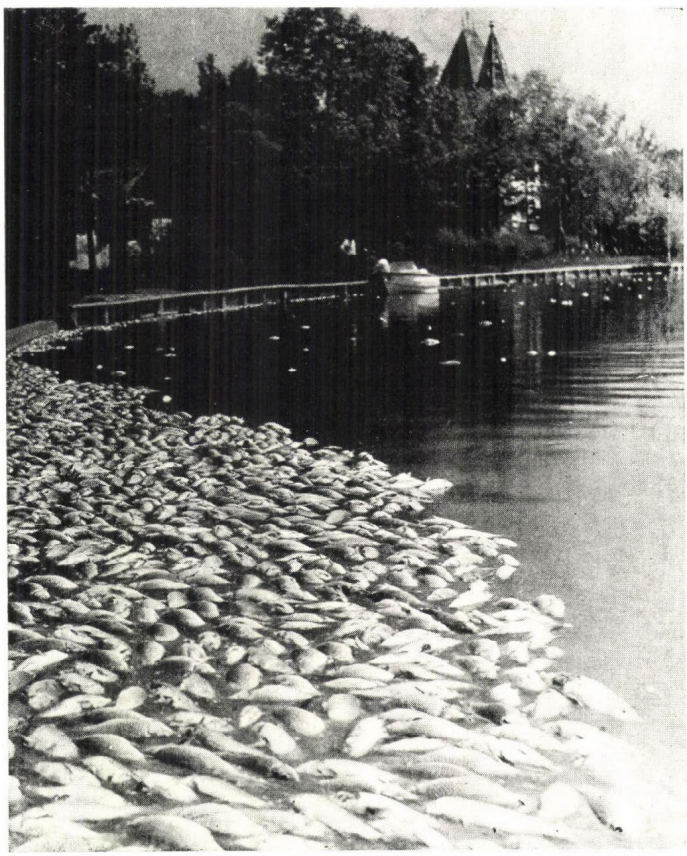

Fig. 3. Wind-collected dead fish on the northern bank of the lake

Of the above cases it was this latter which happened in the case of the lake at Palić, when the hydrogen sulphide, formed as a result of intensive sulphate reduction, led to the destruction of fish and aquatic plants in the entire lake. The death of the fish began on May 7th, 1971, at the western edge of the lake, the process spreading over the entire lake (Fig. 2).

Initially, only a few dead fish were observed on the water surface, the wind and the movement of the water driving some of these to the northern banks (Fig. 3).

The area of the lake is 560 hectares, and the chemical protection of such a large region cannot be realized. The only possibility was the rapid removal of the still living fish. In this way a considerable number of fish could be saved, though several hundred quintals were lost.

Fig. 4. A half-submerged boat containing green algae

To elucidate the cause of fish destruction, or more precisely, the process giving rise to this, was greatly facilitated by the fact that systematic investigations had been conducted to discover the microbiological processes of the lake in the preceding years. These investigations and the consideration of our earlier experiences, together with examinations made at the time of the fish destruction, all led invariably to the conclusion that the fish had been killed by some compound produced by the natural processes in the lake.

It was necessary to establish this fact, primarily because it could also be possible that insecticides, among them lindane, had been responsible for the damage. The observations which led us to discount the effects of pesticides were as follows:

1. A half-submerged boat was found in front of one of the farms at the bank (Fig. 4). There were green algae in the boat but nowhere else at all. The wooden sides of the boat prevented hydrogen sulphide to penetrate and exert effect on the green algae, therefore they remained alive.

2. The fish being recovered from the lake still alive, but in a state of torpor, revived in storage tanks well provided with oxygen, and practically 100 per cent of these fish remained alive. This experience excluded the insecticides from the list of possible causes. The trouble was therefore due to a general poison, harmful to all living organisms.

The processes leading to the destruction are outlined below.

In the course of years, a very fine mud of town origin, with a high organic matter content, had been deposited at the bottom of the lake, in some places attaining a depth of 1 m. All the necessary conditions were given in this very fine mud for the sulphate-reducing bacteria to produce hydrogen sulphide.

The hydrogen sulphide combined with the iron present in the mud produced iron sulphide and it accumulated. The amount of sulphide ($S^{2-}$) in the mud samples was 23–78 mg per 100 g wet mud. However, the formation of hydrogen sulphide still continued even when neither the mud nor the water contained available iron for the binding of hydrogen sulphide which accumulated there in a gaseous form. The subtropical weather at the end of April and at the beginning of May 1971 intensified the activity of the bacteria and the production of hydrogen sulphide, which, as a result of the decrease in air pressure rose into the water layer (Vámos 1966). In this concentration it began to destroy the blue algae, large masses of which had previously limited water transparency to at most 15 cm. The dead algae sank to the bottom. Consequently, the water became clearer, its transparency later increasing. Such a clear water had for many years not been observed in the lake at Palić. Although the water was clear, it contained no, or only a minimal, amount of oxygen. The water was stained red by the carotene produced by *Daphnia magna* under the oxygen-deficient conditions. Different areas were of a creamy-yellow colour owing to the precipitating sulphur. Oxygen was consumed by the oxidation of hydrogen sulphide and by sulphur and other bacteria decomposing the dead mass of algae. As a result of the disturbed life functions of algae, there was a marked deficiency in the oxygen produced by photosynthesis. In such an oxygen-deficient environment the oxidation and neutralization of hydrogen sulphide ascending in the water layer were very slow. In addition, a further unfavourable consequence ensued. In the absence of oxygen, the toxic concentration of hydrogen sulphide for fish was substantially lower being merely a few tenths of a mg per litre.

From a chemical point of view it is interesting that the amount of dissolved phosphorus increased significantly. The change is all the more striking when compared with data collected prior to the perishing of fish. In samples taken at 10th September, 1970, the $P_2O_5$ content was only 0.12–0.75 mg per l. This concentration decreased from west to east. At the time of the death of the fish not only the $H_2S$ concentration but also the $P_2O_5$ concentration rose markedly to 0.5–1.1 mg per l with the same concentration gradient as before. The increased phosphate was chiefly derived from soluble phosphate ion by the chemical activity of $H_2S$ on insoluble iron and manganese phosphates in the mud.

These conditions developed on or about 4th May, 1971, when the fish were poisoned. The dead fish first appeared on the water surface on 7th May, near the Vecsernyés farm, where the mud layer is about 1 m thick and the smell of hydrogen sulphide prevailed above the lake for more than a week. As a result of the $H_2S$ poisoning the fish sank head downwards into the mud with open gills and remained vertically embedded.

The fish stock in the lake consisted almost entirely of wild carp averaging

in weight between 40 and 70 dkg. Only very few individuals could be observed the weight of which was around 1 kg, these being 6–8-year-old specimens. The cause of the suspended development was a lack of food. The larvae and worms playing an important part in the supply of natural food were absent from the mud. This is understandable, since oxygen was completely absent from the mud, the surface of which was black due to iron sulphide. The redox level was thus not in the mud, but higher up, in the water layer. Such conditions are not suitable for the production of fish food of live organisms.

Fig. 5. The drained lake bed

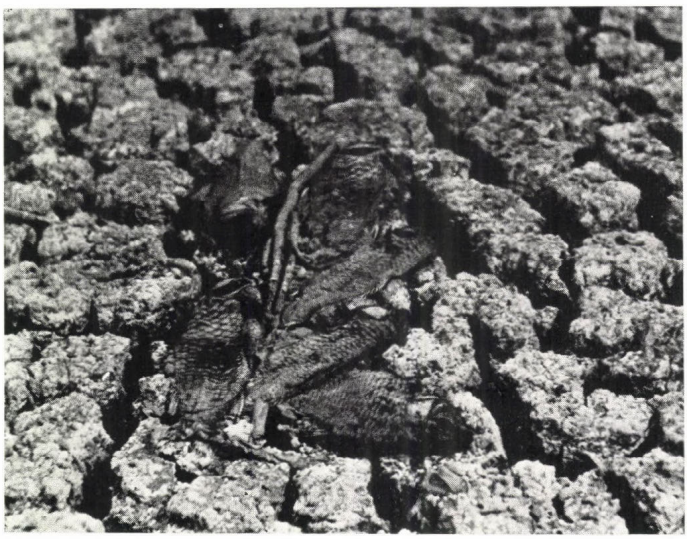

Fig. 6. Dead carp on the drained bed

The lake has been drained (Figs 5, 6), since without this drastic intervention no oxidation of the reduced mud could be expected, thus no construction work necessary for the rejuvenation of the lake could be performed. The penetration of air is promoted by larvae and worms burrowing in the drying mud (Fig. 7).

Fig. 7. Larvae and worms burrowing in the drying mud

The drainage was an unavoidable intervention to restore the lake to the condition it had been in at the turn of the century, when Palić was a favourite bathing place. The first signs of eutrophication appeared about 30 years ago.

Why has the lake changed? The reason for this may be expressed in the following: man poisons his own environment. This has been so in the case of the lake at Palić, too.

## FACTORS OF POLLUTION

Subotica, being an agricultural centre at the turn of the century, is at present an industrialized large town, supplied with a good drainage system. Recently, an increasing number of factories and plants began production. The waste-water of the town and the plants, that of a large abattoir and a factory producing fertilizers and of a galvanizing works entered the lake. Owing to the insufficient purification of water, the amount of organic matter in the lake increased, as did the quantities of sulphate and phosphate ions. The original sulphate content rose from 60 to 800 mg per litre.

Perhaps nowhere was the sulphatizing of lakes more dangerous than in the Danube basin. The lake at Palić was originally a hydrocarbonate-type lake, similar to Lake Fehér near Szeged. Some years back the soda effloresc-ing on the drying-out banks was collected and used in soap-making. Today

there is not even a gramme of soda at the sulphate-type, dried-out bottom of the lake. The high sulphate content and the organic contamination led to an intensive sulphate reduction, and hydrogen sulphide was formed, this compound destroying the lake at Palić with fish and all. This has been a typical case of environmental pollution.

The outline scheme of the reconstruction is as follows (Fig. 8):

Activated sludge biological waste-water purifier (1); surface aeration of oxidation lakes (2); fish lakes (3); from which completely purified water passes into the bathing part of the lake (4) destined for bathing, boating and fishing.

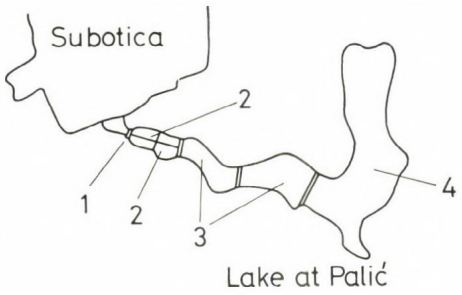


Fig. 8. Outline scheme of the reconstruction (for explanation of numbers see text)

The work of rejuvenating the lake at Palić is in progress and it is hoped that in the near future all natural conditions will be restored.

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*Symp. Biol. Hung.*, *15*, pp. 189–193 (1975)

# SODA AND $H_2S$ FORMATION IN ALKALI LAKES

by

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One of the methods of utilizing alkali lakes and unproductive alkali soil is the construction of fish ponds. This is one of the issues of the Hungarian fisheries development programme. To achieve this a detailed knowledge of the properties of alkali soils and their processes under waterlogging is necessary.

In Hungary, sodic lakes and sodic alkali soils (solonchak) can be found only where soils contain lime in their surface layers, mainly on the deposit of the Danube (Fig. 1).

On the other hand, there are no such lakes and soils on the Tisza deposits, the soils being solonetz and containing no lime in their surface layer.

On drying out solonchak-type soils, soda crystallizes out from the mud (Fig. 2). In the case of solonetz soils this has never been observed.

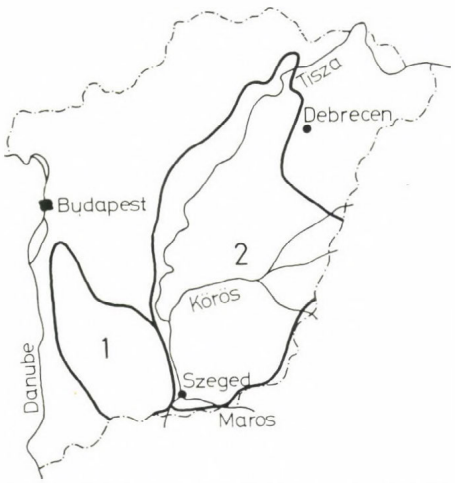


Fig. 1. Distribution of alkali soils in the Great Hungarian Plain. 1 = solonchak; 2 = solonetz-type soils

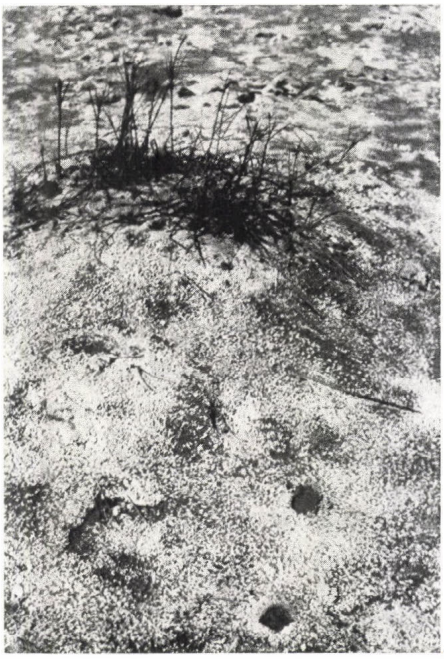

Fig. 2. Soda crystallizes out in the dry period on solonchak soils

Every research worker dealing with alkalization agrees that the formation of alkali soil and soda occurs in soils periodically covered with water. In connection with the origin of soda it was noted as early as 1839 by Irinyi that in nature soda does not form through inorganic reactions. The theories put forward in favour of inorganic soda formation at the turn of the century have never been confirmed. Many other workers (Treitz 1923, 'Sigmond 1923) suggested that alkalization and soda formation are due to hydrobiological processes in the mud. Treitz (1923) was the first to attribute a role to the biological sulphate reduction in soda formation in stagnant water.

The results of some of our studies have been reported earlier (Vámos 1955, 1964), concerning the role of bacteriological processes in the formation of soda. The previous works did not fully elucidate the role of lime, therefore the present work discusses this problem.

## CHANGES IN THE MUD

In submerged soils the decomposition of organic matter starts in spring with the rising of temperature. Under optimal circumstances bacteria rapidly proliferate and their number may even reach more than a hundred or thousand times the original amount. In this process the quality of the decomposing organic matter and temperature play an important role. The abundant reserves of organic and inorganic nitrogen in the soil may stimulate the growth of bacteria. Under favourable circumstances the proliferation of bacteria entails intensive oxygen consumption. The reduction of nitrates commences with the disappearance of oxygen, and at about the same time the reduction of manganese and iron oxides starts as well. This is followed later—at a lower redox potential—by the reduction of sulphates and phosphates (Bloomfield 1969).

Since the mud solution and the water contain only a few mg of nitrate and still less phosphate ions, the changes taking place in the water and the mud and later in the soil, are mainly due to the reduction of sulphate ions being present in abundance.

The reduction processes are associated with the decomposition of organic materials. The electrons produced by the respiration of bacteria transform manganese and iron oxides, as acceptors, to soluble $Mn^{2+}$ and $Fe^{2+}$ ions (Vámos and Andó 1969, Vámos and Tasnádi 1972).

Under anaerobic conditions the decomposed organic matter and the residues of floral origin are accompanied by the production of organic acids and gases, mostly methane, containing also small amounts of carbon dioxide, nitrogen, and hydrogen (Yamane and Sato 1963). The short-chain carboxylic acids produced via the glycolytic decomposition are used up not only by reduction but also by methane bacteria. Under $Eh_0O$ mV an intensive reduction process begins the required energy of which is partly supplied from hydrogen produced by *Clostridia*, mainly by *Cl. felsineum*, forming a yellow pigment.

Besides utilizing hydrogen, the sulphate-reducing bacteria need carbon in the form of organic compounds. A source of energy for sulphate-reducing bacteria could be ethanol, lactic, butyric or pyruvic acids, with the excep-

tion of acetic acid (Starkey 1966). The most common equations for sulphate reduction are as follows:

$$Na_2SO_4 + 4H_2 \xrightarrow{H_2O} NaOH + NaSH + 4H_2O$$

$$NaSH + H_2CO_3 \longrightarrow NaHCO_3 + H_2S$$

As a result of sulphate reduction, sodium hydrocarbonate and hydrogen sulphide are produced. The right-hand side of the second equation can be seen in Fig. 3.

During the evaporation of water, i.e. during desiccation, owing to a decreasing $CO_2$ tension, sodium hydrocarbonate comes to the surface, and it turns into soda on the shore and in plant residues (Fig. 4). This is the phenomenon of 'soda blooming' on the uneven, limy, sandy surface. Thus, soda is formed from hydrocarbonate during desiccation, this being the origin of the Hungarian word *szikső* (desiccated salt). $H_2S$ produces FeS by reacting with $Fe^{2+}$ ions and iron oxide (Fig. 5).

Under aerobic conditions, the ferrous sulphide is oxidized to sulphuric acid. The simplified equation for sulphide oxidation, consisting of several steps, may be written as follows:

$$S^{2-} + 2O_2 \longrightarrow SO_4^{2-}$$

$H_2SO_4$ releases $H_2S$ from FeS, and this gas can cause fish destruction and root rot of the rice plant (Vámos 1964). On the other hand, $H_2SO_4$ can reconvert soda to Glauber's salt. In this process the presence or absence of lime plays an important role, since $H_2SO_4$ is neutralized by reacting with lime, and gypsum is formed. The lime protects the soda and with time the amount of soda increases. In the dry period, it crystallizes on the soil surface, this is how solonchak-type soils develop.

In soils with no lime in their surface layer, but rich in iron, during the waterlogging much FeS accumulates in the mud. $H_2SO_4$ formed under aero-

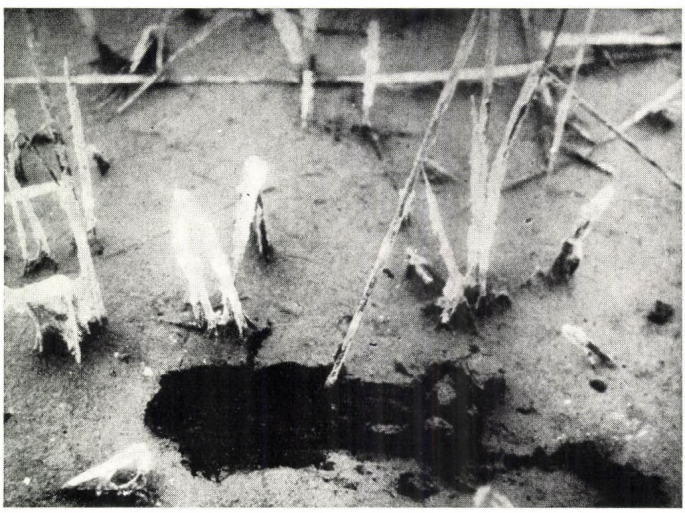

Fig. 3. 'Soda blooming' on plant residues and ferrous sulphide formation in the mud

Fig. 4. 'Soda blooming' on plant residues


Fig. 5. Ferrous sulphide under the surface layer containing soda

bic conditions from the FeS weathers the minerals and carries the dissolved salts into deeper layers. This is the essence of the development of solonetz-type soils.

The various alkali soil profiles are thus hydrobacteriological formations, i.e. they were formed as a result of processes of periodic waterlogging.

In the utilization of lakes on alkali soils for fish production, it is important therefore to take into account whether the soil is of the solonchak or solonetz type. In the former case, the water of the lake is characterized by a high pH value being often around 10. In this case the formation of free

ammonia is a danger, particularly at the time of the decomposition of water plants, in July. An example of this type of lake is Lake Fehér near Szeged and a number of lakes between the Danube and the Tisza.

In lakes on solonetz-type soil, however, where the abundance of iron enables the accumulation of FeS, the danger is incurred by the release of quantities of $H_2S$ poisonous to fish. For example, such lakes are those at Biharugra and all backwaters of the rivers Tisza and Körös.

In these ponds and backwaters, and in all other ponds in which the amount of organic matter constantly increases, a simultaneous increase of the quantity of sulphate ions adds to the danger. $H_2S$ formed by sulphate reduction may entirely exterminate lacunar life.

Mass death of fish, in which all the fish stock perished due to $H_2S$, occurred especially in barrage ponds.

The recognition of these phenomena considerably simplified the protective work and, in many cases, the prevention of the loss of many tons of fish.

## SUMMARY

According to 'Sigmond (1923) the fundamental factors of alkalization are as follows: (1) warm, dry climate, (2) periodical waterlogging and (3) water-impermeable layer in the soil. The simultaneous presence of these factors results partly in the accumulation of salts, and on the other hand, gives rise to microbiological processes which may lead to soda and hydrogen sulphide formation. Both products of the sulphate reduction have unfavourable effects on the quality of water and on the development of fish.

Soda raises the pH value, and in the case of a high ammonium content this can lead to the death of fish through the formation of free ammonia.

As a general cell enzyme and nerve poison, in higher concentration hydrogen sulphide destroys all the living creatures unable to escape from the water. In lower concentration, it merely inhibits their metabolism and development.

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# III. SECONDARY PRODUCTION

*Symp. Biol. Hung.*, *15*, pp. 197–204 (1975)

# THE INFLUENCE OF FLUCTUATING TEMPERATURE ON PLANKTON ROTIFERS. A GRAPHICAL MODEL BASED ON LIFE DATA OF *HEXARTHRA FENNICA* FROM NEUSIEDLERSEE, AUSTRIA

by

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In September 1972, a Symposium on the influence of temperature on organisms was held in Obergurgl, Austria. At this meeting it was extensively discussed how fluctuating temperature influences the reaction of an organism, whether it is permissible to average the temperature differences and to calculate the reaction according to the mean temperature, or whether the temperature responses are always shifted irregularly as it was found by Kaufmann (1932) who used the log-phase growth of insect larvae for his experiments.

This question is particularly important as far as plankton organisms are concerned, for two reasons:

1. Calculations of production inevitably involve temperature factors, as for example, Edmondson's (1960) famous birth rate formula for plankton rotifers: $b = \frac{E/f}{D/t}$ ; the same is true for calculations of generation time or of turnover time of any phyto- or zooplankton.

2. If fluctuating temperature results in an uneven life cycle of plankton organisms, this may lead, to a certain extent, to the synchronization of biological activities such as cell division, egg deposition and the like. All these parameters are important for plankton counting, measurements of biomass and estimation of standing crop; hence, time of day and frequency of sampling may become increasingly important.

Although daily temperature fluctuations occur in every body of water, they are probably of little importance to organisms in large deep lakes and in a moderate climate. However, in shallow waters, in the littoral zone, and under extreme climatic conditions, these fluctuations may reach a wide amplitude and last over a long period of time thus considerably influencing the life cycle of the phyto- and zooplankton species of that particular body of water. For this reason we used data for our considerations of a rotifer, *Hexarthra fennica* from Neusiedlersee, where in summer daily temperature fluctuations of 5 °C occur frequently over a period of several days and where even differences up to 10 °C occur occasionally* (Fig. 1).

We have been cultivating *Hexarthra fennica* for several years in our laboratory in Lunz at temperatures of 15 °C, 20 °C and 25 °C on a diet of *Chlo-*

* My thanks are due to Dr. O. Motschka, Z. A. f. Meteorologie, Vienna, for kindly providing temperature data of Neusiedlersee.

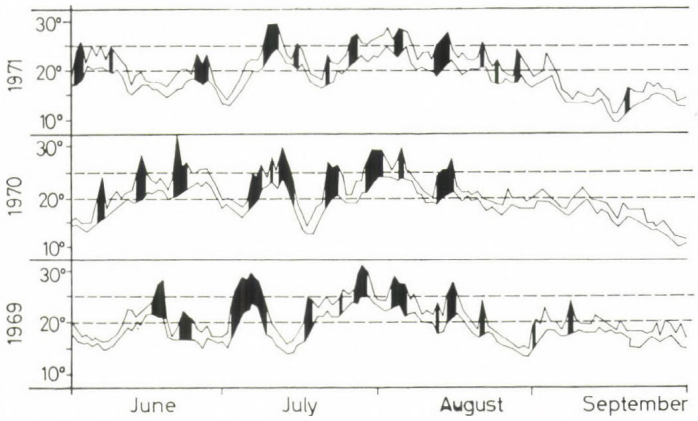


Fig. 1. Daily max and min temperatures in Neusiedlersee, Austria during the summer months of 1969–1971. Black parts indicate temperature differences of more than 5 °C

*rella vulgaris* (Ruttner-Kolisko 1971). Under constant conditions and with approx. $10^6$ *Chlorella* cells per ml, *Hexarthra* reproduces parthenogenetically in a very regular way showing an extremely uniform pattern of life cycle, which we have verified in many individual cultures.* From these cultures the following mean values for the most important life data have been calculated (Table 1).

TABLE 1

| *Hexarthra fennica* (mean values, in h) | 15 °C | 20 °C | 25 °C |
|---|---|---|---|
| Egg development time, $D$ | 36 | 17.5 | 8.5 |
| Interval between eggs, $I$ | 25.5 | 9.5 | 3.5 |
| Period of immaturity, $Im$ | 86 | 45 | 25 |
| Generation time $(Im + D)G$ | 122 | 62.5 | 33.5 |
| (approx.) length of life, $L$ | 300 | 150 | 100 |
| Number of eggs, $N$ | 10–12 | | |

Plotted on semilog paper against temperature (Fig. 2) all mean values fit extremely well into straight lines, thus clearly showing the exponential temperature dependence of metabolic processes—a general postulate which has been well known for a long time. The temperature difference necessary for doubling the speed of metabolism of *Hexarthra fennica* in an abundance of food is approx. 5 degrees (4.8 °C for egg development).

As shown in Fig. 1, daily temperature fluctuations of 5 °C or more occur in Neusiedlersee in summer at temperatures around 25 °C. We chose, there-

* For reliable technical assistance and vivid interest in the work I am grateful to Miss E. Kronsteiner.

fore, as our model a uniform 24-h fluctuation between 25 °C at 2 p.m. and 20 °C at 2 a.m. The individual values for the life data corresponding to the particular temperatures at each hour were established by using the graph of Fig. 2 (but on a larger scale) as a nomogram for interpolation between data known from experiments. This procedure was thought permissible owing to the very strict life pattern of rotifers in the parthenogenetic phase, confirmed by our culture experiments. Starting from those figures, the corresponding life data $D/f$, $I/f$, $Im/f$ and $G/f$ for fluctuating temperatures

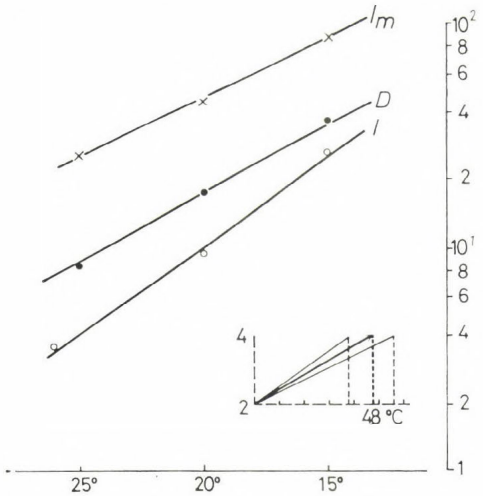


Fig. 2. Temperature dependence of egg development time ($D$), interval between eggs ($I$) and period of immaturity ($Im$) in cultures of *Hexarthra fennica* in an abundance of food

have been calculated by summing up the respective portions for each particular hour. All the necessary data for our further considerations are compiled in Table 2.

As an example of the operation used, the egg development time $D$ is indicated for each hour in Fig. 3: above the line: for the temperature oscillating between 20 °C and 25 °C, below the line: for the temperature of that particular time of the day remaining constant. The difference between the egg development time at constant and at fluctuating temperature ($D/k - D/f$) is $-4.5$ h at 5 p.m. and $+5.6$ h at 4 a.m. which amounts to nearly 50 per cent and over 30 per cent, resp. of the constant development time $D/k$. This shows already clearly that under the conditions we have chosen for our model the use of the actual temperature at sampling time for production calculations may lead to considerable errors.

In the following graph (Fig. 4) $k$- and $f$-values for the most important life parameters $D$, $I$, $Im$, $G$ as well as the deviation of $f$- from $k$-values have been plotted for every hour of the day. From this graph three facts are obvious: the more time a particular parameter covers the wider are the fluctuations of its $k$-values during the 24-h temperature oscillation; but at the same time the $f$-values are more and more straightened out to the value of the mean temperature. In contrast to that, the deviation of $f$-values

TABLE 2

| Time of day/h | Temperature at time h (°C) | Life data at constant temperatures | | | | | | | | Life data at fluctuating temperatures starting from the respective h | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | ($k$/h) | | | | 100 $k$ 1 h in per cent of $k$-value | | | | | | | |
| | | $D/k$ | $I/k$ | $Im/k$ | $G/k$ | $D/k$ | $I/k$ | $Im/k$ | $G/k$ | $D/f$ | $I/f$ | $Im/f$ | $G/f$ |
| 8 | 22.5 | 12.2 | 5.7 | 33.5 | 45.7 | 8.2 | 17.6 | 3.0 | 2.2 | 9.5 | 4.6 | 31.5 | 44.3 |
| 9 | 23.2 | 11.1 | 5.0 | 31.0 | 42.1 | 9.0 | 20.0 | 3.2 | 2.4 | 9.5 | 4.2 | 31.0 | 44.3 |
| 10 | 23.8 | 10.2 | 4.5 | 28.8 | 39.0 | 9.8 | 22.4 | 3.5 | 2.5 | *9.0* | 4.0 | 31.0 | 45.0 |
| 11 | 24.3 | 9.5 | 4.1 | 27.2 | 36.7 | 10.5 | 24.4 | 3.7 | 2.7 | 9.5 | 3.8 | *30.9* | 45.4 |
| 12 | 24.7 | 8.9 | 3.7 | 26.0 | 34.9 | 11.2 | 26.9 | 3.8 | 2.8 | 10.0 | 3.6 | 31.0 | 45.5 |
| 13 | 24.9 | 8.6 | 3.6 | 25.2 | 33.8 | 11.6 | 28.0 | 4.0 | 2.9 | 10.3 | *3.5* | 31.0 | 45.5 |
| 14 | 25.0 | *8.5* | *3.5* | *25.0* | *33.5* | 11.8 | 28.5 | 4.0 | 3.0 | 11.0 | 3.6 | 31.5 | *45.5* |
| 15 | 24.9 | 8.6 | 3.6 | 25.2 | 33.8 | 11.6 | 28.0 | 4.0 | 2.9 | 12.3 | 4.0 | 32.0 | 45.5 |
| 16 | 24.7 | 8.9 | 3.7 | 26.0 | 34.9 | 11.2 | 26.9 | 3.8 | 2.8 | 13.3 | 4.3 | 32.5 | 45.3 |
| 17 | 24.3 | 9.5 | 4.1 | 27.2 | 36.7 | 10.5 | 24.4 | 3.7 | 2.7 | 14.0 | 5.0 | 33.5 | 45.3 |
| 18 | 23.8 | 10.2 | 4.5 | 28.8 | 39.0 | 9.8 | 22.4 | 3.5 | 2.5 | 14.5 | 6.0 | 34.0 | 45.0 |
| 19 | 23.2 | 11.1 | 5.0 | 31.0 | 42.1 | 9.0 | 20.0 | 3.2 | 2.4 | *14.5* | 7.0 | 34.5 | 44.9 |
| 20 | 22.5 | 12.2 | 5.7 | 33.5 | 45.7 | 8.2 | 17.6 | 3.0 | 2.2 | 14.5 | 7.9 | 35.0 | 44.8 |
| 21 | 21.9 | 13.4 | 6.5 | 36.0 | 49.4 | 7.5 | 15.4 | 2.8 | 2.0 | 14.0 | 8.3 | *35.0* | 44.5 |
| 22 | 21.3 | 14.6 | 7.3 | 38.6 | 53.2 | 6.9 | 13.7 | 2.6 | 1.9 | 14.0 | *8.5* | 35.0 | 44.5 |
| 23 | 20.8 | 15.7 | 8.1 | 41.0 | 56.7 | 6.4 | 12.3 | 2.4 | 1.8 | 13.5 | 8.4 | 34.5 | 43.7 |
| 24 | 20.4 | 16.6 | 8.8 | 43.0 | 59.6 | 6.0 | 11.4 | 2.3 | 1.7 | 13.0 | 8.2 | 34.3 | 43.3 |
| 1 | 20.1 | 17.2 | 9.2 | 44.5 | 61.7 | 5.8 | 10.9 | 2.3 | 1.6 | 12.7 | 7.9 | 34.0 | 43.4 |
| 2 | 20.0 | *17.5* | *9.5* | *45.0* | *62.5* | 5.7 | 10.7 | 2.2 | 1.6 | 12.0 | 7.4 | 33.6 | 43.4 |
| 3 | 20.1 | 17.2 | 9.2 | 44.5 | 61.7 | 5.8 | 10.9 | 2.3 | 1.6 | 11.7 | 7.0 | 33.0 | *43.0* |
| 4 | 20.4 | 16.6 | 8.8 | 43.0 | 59.6 | 6.0 | 11.4 | 2.3 | 1.7 | 11.0 | 6.5 | 32.8 | 43.1 |
| 5 | 20.8 | 15.7 | 8.1 | 41.0 | 56.7 | 6.4 | 12.3 | 2.4 | 1.8 | 10.7 | 6.0 | 32.5 | 43.2 |
| 6 | 21.3 | 14.6 | 7.3 | 38.6 | 53.2 | 6.9 | 13.7 | 2.6 | 1.9 | 10.2 | 5.4 | 32.0 | 43.5 |
| 7 | 21.9 | 13.4 | 6.5 | 36.0 | 49.4 | 7.5 | 15.4 | 2.8 | 2.0 | 9.8 | 5.0 | 31.7 | 43.8 |
| 8 | 22.5 | 12.2 | 5.7 | 33.5 | 45.7 | 8.2 | 17.6 | 3.0 | 2.2 | 9.5 | 4.6 | 31.5 | 44.3 |

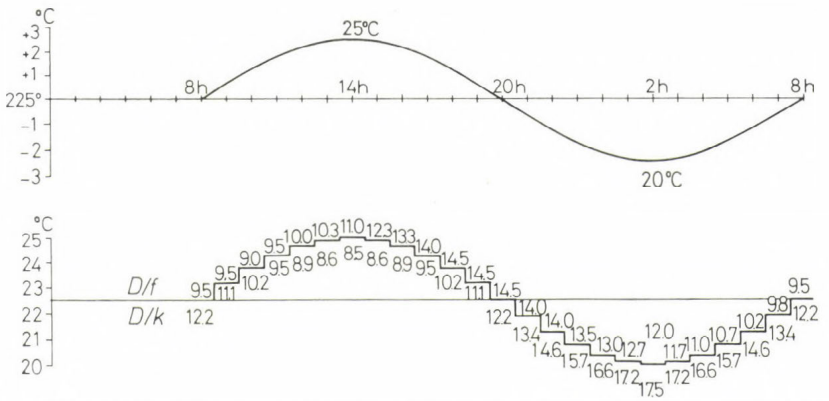


Fig. 3. Upper part: nomogram of a 24-hour temperature oscillation between 20 °C and 25 °C. Lower part: egg development time for each hour; $D/f$ = calculated for fluctuating temperature, $D/k$ = calculated for the constant temperature of the particular hour

Difference between constant and fluctuating temperatures

| Abs. temperature values (in h) | | | | Deviation ($d$) in per cent of $k$-values | | | |
|---|---|---|---|---|---|---|---|
| *D/k–D/f* | *I/k–I/f* | *Im/k–Im/f* | *G/k–G/f* | *D/k–D/f* | *I/k–I/f* | *Im/k–Im/f* | *G/k–G/f* |
| +2.7 | +1.1 | + 2.0 | + 1.4 | +22.1 | +19.4 | + 6.0 | + 3.1 |
| +1.6 | +0.8 | 0 | − 2.2 | +14.4 | +16.0 | 0 | − 5.3 |
| +1.2 | +0.5 | − 3.2 | − 6.0 | +11.8 | +11.2 | −11.2 | −15.0 |
| 0 | +0.3 | − 3.7 | − 8.7 | 0 | + 7.3 | −13.7 | −23.5 |
| −1.1 | +0.1 | − 5.0 | −10.6 | −12.3 | + 2.8 | −19.0 | −29.7 |
| −1.7 | 0 | − 5.8 | −11.7 | −19.7 | 0 | −23.2 | −33.9 |
| −2.5 | −0.1 | − 6.5 | *−12.0* | −29.5 | − 2.8 | −26.0 | *−36.0* |
| −3.7 | −0.4 | *− 6.8* | −11.7 | −42.9 | −11.2 | −27.2 | −33.9 |
| −4.4 | −0.6 | − 6.5 | −10.4 | *−49.3* | −16.1 | −24.7 | −29.1 |
| *−4.5* | −0.9 | − 6.3 | − 8.6 | −47.3 | −24.0 | −23.3 | −23.2 |
| −4.3 | −1.5 | − 5.2 | − 6.0 | −42.1 | −33.6 | −18.2 | −15.0 |
| −3.4 | −2.0 | − 3.5 | − 2.8 | −30.6 | *−40.0* | −11.2 | − 6.7 |
| −2.3 | −2.2 | − 1.5 | + 0.9 | −18.9 | −38.8 | − 4.5 | + 2.0 |
| −0.6 | −1.8 | + 1.5 | + 4.9 | − 4.5 | −27.7 | + 4.2 | + 9.8 |
| +0.6 | −1.2 | + 3.6 | + 8.7 | + 4.1 | −16.4 | + 9.4 | +16.5 |
| +2.2 | −0.3 | + 6.5 | +13.0 | +13.1 | − 3.7 | +15.8 | +23.4 |
| +3.6 | +0.5 | + 8.7 | +16.3 | +21.6 | + 5.7 | +20.0 | +27.7 |
| +4.5 | +1.3 | +10.5 | +18.3 | +26.1 | +14.2 | +24.2 | +29.3 |
| +5.5 | +2.1 | +11.4 | *+19.1* | +31.4 | +22.5 | +25.1 | +30.6 |
| +5.5 | +2.2 | *+11.5* | +18.7 | +31.9 | +24.0 | +26.5 | +30.5 |
| *+5.6* | *+2.3* | + 9.2 | +16.5 | *+33.6* | +26.2 | +21.2 | +28.5 |
| +5.0 | +2.1 | + 8.5 | +13.5 | +32.0 | *+26.8* | +20.4 | +24.3 |
| +4.4 | +1.9 | + 6.6 | + 9.7 | +30.4 | +26.0 | +17.2 | +18.4 |
| +3.6 | +1.5 | + 4.3 | + 5.6 | +27.0 | +23.1 | +12.0 | +11.2 |
| +2.7 | +1.1 | + 2.0 | + 1.4 | +22.1 | +19.4 | + 6.0 | + 3.1 |

in per cent of the respective $k$-values is similar in each case, amounting approx. from −40 per cent to +30 per cent. This result has to be considered *in praxi*: dealing with parameters the duration of which covers the time of temperature fluctuation or more than that, values applying to the mean temperature of the oscillation can be used for calculations without making a big error; but with parameters of short duration or with organisms having a short life time compared with the daily temperature cycle the shifted data for fluctuating temperatures should be applied.

The other point of view which makes temperature fluctuations an interesting limnological feature is the question whether or not it induces synchronization of the biological activities of plankton organisms and if so, to what extent. Using again the data calculated from our culture experiments and compiled in Table 2, we started with the assumption of evenly distributed eggs in a *Hexarthra* population exposed to fluctuating temperatures in a 24-h rhythm (Fig. 5). According to the changing development times, these eggs will hatch unevenly, resulting 50 per cent of the newborn individuals crowded within 6.5 hours (while the temperature is highest), the other 50 per cent being scattered dividing the rest of the 24 hours of the day. As a consequence, the first eggs of the next generation are also unevenly distrib-

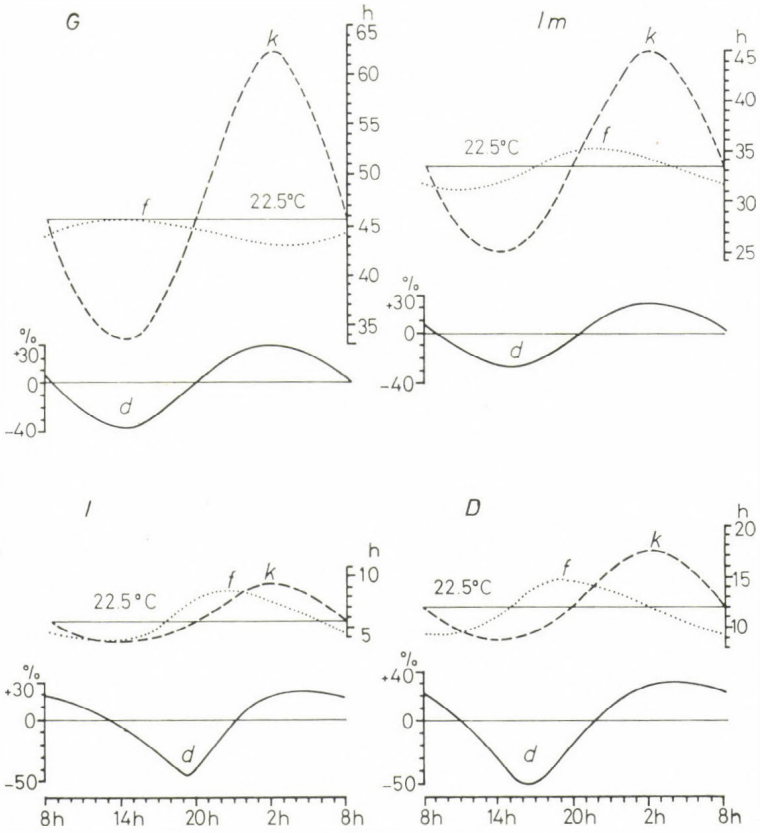


Fig. 4. Deviation ($d$) of the respective $f$-values from $k$-values ($k$–$f$) for the main life parameters $D, I, Im$, and $G$ during the 24-hour temperature oscillation, expressed in per cent of the $k$-values (for further explanation see text)

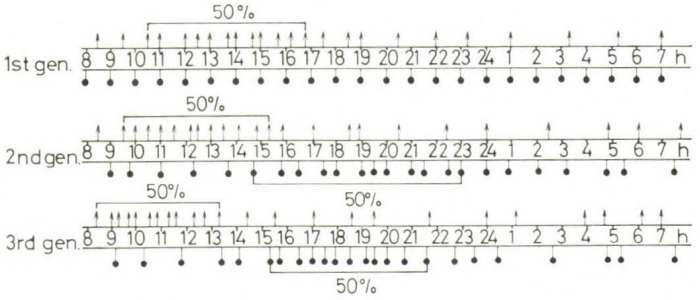


Fig. 5. Schedule of egg deposition (↓) and hatching (↑) in 3 generations of *Hexarthra fennica* exposed to temperatures fluctuating daily between 20 °C and 25 °C

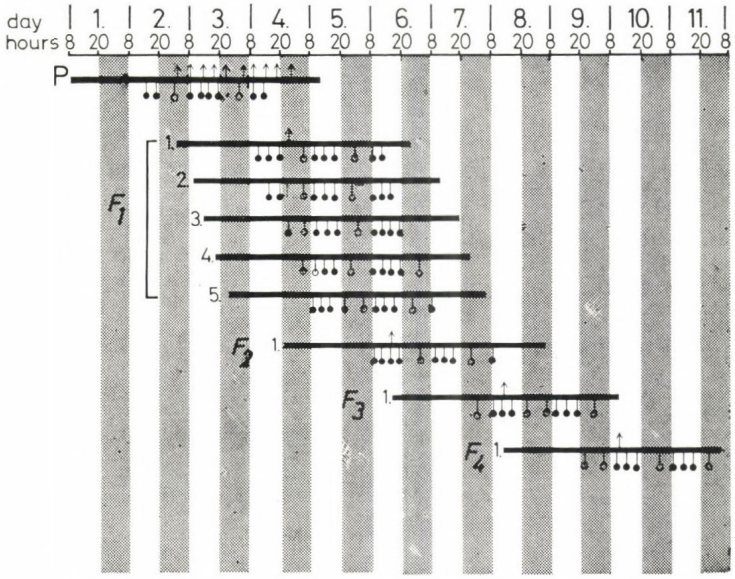


Fig. 6. Schedule of egg deposition in a clone derived from one individual ($P$) exposed to temperatures fluctuating daily between 20 °C and 25 °C. Black dots: eggs deposited during the 12 hours above mean temperature; white dots: eggs deposited in the time below mean temperature

uted, 50 per cent occurring within 8 hours only and the newborns being packed even closer (50 per cent in 6 h). The same trend characterizes the third generation with half of the eggs laid within 6.5 hours and half of the newborns hatching within 5 hours of the day. Without extending the model any further, the tendency to shorten the interval between both eggs and hatchlings becomes obvious.

This must finally lead to a more or less complete synchronization, the rhythm and completeness of which will naturally depend not only on the regularity of the life data of the plankton organism in question but also on the amplitude and duration of the temperature fluctuation. Mainly in shallow tropical lakes, where regular temperature oscillations occur over long periods, such synchronizations should be considered, and have already been recorded.

The diagram of Fig. 5 deals only with generations following one another, but omits the successive eggs of one female. To show the effect of fluctuating temperature on the offspring of one particular individual, we have built up a hypothetical clone using again the tabulated data (Fig. 6). In the parental generation, times of egg deposition as well as hatching times are indicated in order to get the starting points of $F_1$-life histories. Further on, only the eggs and the hatchling of the first egg are marked. With temperature oscillations, according to our schedule, egg deposition swings immediately into a rhythm, with three of the four eggs per 24 hours being laid during the 12 hours above mean temperature and only one egg during the same length of time below mean temperature. This rhythm is maintained not only with all

the individuals of the $F_1$ but also with those of further generations. Thus sampling time becomes very important as far as counts, age structure and egg ratios are concerned.

Both graphs suggest that fluctuating temperature induces not only a rhythmic egg deposition in the life of each single individual but it also leads to a synchronic swinging of the whole population, the extent and speed of which depend on the life schedule and type of thermic oscillation. Wherever temperature fluctuations occur, they must be considered in any investigation of population dynamics.

Constructing a fairly similar graphical model to describe age distribution and other demographic parameters of rotifer populations, Edmondson (1968) has already stressed that such kinds of models are primarily of theoretical interest. The numerical results cannot be generalized and it would be 'tedious and time consuming' to repeat the modelling for each particular organism in each particular environment. For practical use such a model must be converted into a computer programme suitable for everybody to feed in his own data in order to learn whether or not and to what extent, a particular species is affected by the fluctuations of temperature in a particular body of water.

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*Symp. Biol. Hung.*, *15*, pp. 205–214 (1975)

# AN ASSESSMENT OF SPORT-FISH PRODUCTION POTENTIAL IN TWO SMALL ALPINE WATERS IN ALBERTA, CANADA

by

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Primary and secondary production were assessed for a small alpine lake (altitude 2320 m) and a small subalpine pond (altitude 2030 m) in the Rocky Mountains in Alberta, Canada. These studies were part of a re-evaluation of the sport-fishing potential of some small, high-altitude waters in the western Canadian National Parks.

Estimates of total annual primary production per unit surface area were similar for the two waters despite marked differences in patterns of annual production and the fact that the lake is permanent, whereas the pond freezes to the bottom during the winter. In both waters, the main primary consumer was the copepod *Diaptomus tyrrelli* Poppe 1888. The ecological growth efficiencies ($K_1$) of the two copepod populations appear to be similar, although the pond population has two generations per year and the lake population has only one.

The pond contains no fish, but the lake has been recently and fairly heavily stocked with 'trout' species. Present fish production in the lake appears to be extremely low compared to the initial production. The lake before stocking, like the pond now, had a predatory diaptomid species as the main secondary consumer. The fish eliminated these large copepods which have since been replaced by two species of cyclopoid copepods. Reasons for the initial high fish growth rates and the present low growth rates are considered, and an attempt is made to provide a realistic estimate of the production potential on a long-term basis.

There has been some pressure to stock the pond annually on a put-and-take basis. Such stocking is evaluated in terms of production potential, long-range effects on the pond community, and alternate values of the pond. It is likely that reduction of food-organism populations below self-maintaining levels would occur before depletion of nutrients due to biomass export (i.e. fish removal).

The mountain National Parks of western Canada were established comparatively recently. Although the original 'Rocky Mountain National Park' of 25 km$^2$ (10 miles$^2$) was created in 1885 near the present townsite of Banff, it was not until about 40 years later that the mountain Parks began to approach their present size and extent. The first known stocking of fish in the waters of these Parks was in Lake Minnewanka in 1901–2, and stocking has been carried out in selected lakes in the mountain National Parks nearly every year since then. Total numbers of fish stocked and the number of lakes stocked peaked between 1925 and 1935, and again between 1955 and 1965.

Until fairly recently, fishing pressure on these National Park waters remained moderate, even though the number of visitors to the Parks has increased steadily over the years. Problems relative to sport-fisheries have been few; until more recently there were neither obvious needs nor personnel to conduct detailed limnological studies as part of fishery management operations. Great increases in visitor numbers, with concomitant fishing pressures, and an increased public awareness of the impact of man on the environment have emphasized the importance of policies and practices in lake and stream management which are ecologically and conservationally sound.

The initial rapid growth of trout and char stocked in previously fish-free lakes has often been reported (e.g. Nilsson 1972, Rawson 1947). This rapid growth sometimes led to expectations of sustained high productivity which did not materialize in many high-altitude lakes. In some of these, production has declined sharply since the original stocking, although a few lakes have continued to produce reasonably well. Evidence from many other studies (e.g. Fish 1968, Nelson 1964, Rabe 1970, Rawson 1947, Walters 1968) suggests that in the past many lakes may have been stocked too heavily, with the wrong species, or in such a way as to produce an unbalanced fish population—all of which contribute to sub-optimal production.

Large species usually dominate the invertebrate fauna of fish-free alpine lakes in the Canadian Rocky Mountains, and these lakes are often characterized by a relatively large standing-crop biomass. Our studies indicate that many of these species grow slowly and have low production/biomass ($P/B$) ratios, undoubtedly important reasons why fish production after stocking has sometimes failed to stay up to expectations in pristine lakes.

The present project was undertaken to study potential and actual production in two representative alpine waters in Alberta. It was intended as a pilot study for later investigations which would provide management guidelines for standing waters in the mountain National Parks. We hoped to determine which parameters were good indicators of food-organism production and, hence, indicators of potential sport-fish production. Other studies are underway to assess the impact of certain fish species on invertebrate communities in high-altitude lakes.

## THE STUDY AREA

The pond and lake of this study are situated at similar altitudes. At the time of this study, their zooplankton communities were dominated in both numbers and biomass by the same copepod species, *Diaptomus tyrrelli* Poppe 1888. Fish-free before 1960 as far as is known, Snowflake Lake in Banff National Park has been stocked with fish as follows:

1960 — 1000 *Salvelinus fontinalis* Mitchill + 1000 *Salmo gairdneri* Richardson.
1963 — 1000 *S. fontinalis* + 500 *S. gairdneri.*
1964 — 4000 *S. fontinalis* + 1000 *S. gairdneri.*
1965 — 5000 *S. fontinalis* + 5000 *S. gairdneri* + 5000 *Salmo clarki* Richardson.
1966 — 1000 *S. clarki* + 4000 *S. fontinalis.*

No *S. clarki* are known to have survived. So far, we have no evidence of successful natural reproduction of the fish in Snowflake Lake.

Teardrop Pond, south of Banff National Park, is small and shallow. It has never been stocked with fish, although stocking has been advocated at times. These two waters have been described elsewhere (Anderson 1967, 1968, 1970*a*, 1972). Table 1 is a summary of location, morphometric and other features. General locations are given in Fig. 1.


Fig. 1. Map showing the location of the lake and pond

The zooplankton community of Snowflake Lake contained large zooplankton species (>2 mm) before fish stocking, but these species are no longer present. Although there have been recent changes in the constitution of the rotiferan and crustacean plankton, the zooplankton biomass since 1966 has remained fairly constant (Anderson 1972). *D. tyrrelli* has one generation per year; hatching usually occurs in April and most copepods mature in September. Mean generation time is about 115 days. In Teardrop Pond, *D. tyrrelli* produces two generations per year, initial numbers being approximately the same for both generations. Mean generation time is about 90 days. *Diaptomus shoshone* Forbes 1893 and *Eubranchipus intricatus* Hartland-Rowe 1967 are the other two major zooplankters. Each produces one generation per year. There is essentially no winter zooplankton in either of the two waters, except for a small number of cyclopoid copepods in Snowflake Lake.

TABLE 1

*Summary of location and other features for Snowflake Lake and Teardrop Pond, Alberta*

| | Snowflake Lake | Teardrop Pond |
|---|---|---|
| Location | 11U/NH808167 | 11U/PF823630 |
| Elevation | 2320 m | 2030 m |
| Surface area | 7.13 ha | 0.4 ha |
| Depth — maximum | 13.0 m | 1.5 m |
| Depth — mean (June to August) | 6.12 m | 0.6 m |
| Volume (June to August) | $4.36 \times 10^5$ m$^3$ | $2.4 \times 10^3$ m$^3$ |
| Sum of constituents (TDS as ppm) | 102 ppm | 41 ppm |
| pH (0.5 m, July) | 8.1 | 9.7 |
| Dominant anion/cation | $HCO_3$/Ca | $HCO_3$/Ca |
| Open-water season (approx.) | June 25/Oct. 10 | Apr. 25/Oct. 25 (variable) |
| Maximum ice thickness | 1.2 m | freezes to bottom |
| Maximum surface temperature | 13 °C | 18 °C (usually less) |
| Surface inlet | yes | no |
| Surface outlet | yes | no |
| Bottom sediments (% organic) | 20.1% | 11.4% |
| Macrophytes | no | some |
| Fish | yes | no |

## METHODS AND MATERIALS

The radio-isotope methods and materials for assessing primary production were basically those described and provided by the International Agency for $^{14}C$ Determination, Søborg, Denmark. Experiments were carried out several times a year at 5 or 7 depth intervals in Snowflake Lake and usually 2 depths in Teardrop Pond. Production per unit surface area was corrected to account for basin morphometry.

Two or more replicate benthic samples were taken at each sampling site with a 230-$cm^2$ Ekman dredge. Freshweights were measured within one or two days to avoid excessive weight loss (Howmiller 1972). Details of plankton methods have been given elsewhere (Anderson 1971). Vertical and horizontal tows were made with a conical net (mouth diam. = 24 cm; bolting silk aperture 65–70 $\mu$), supplemented with trap samples. Physical and chemical methods have been described earlier (Anderson 1970*a*). Phytoplankton biomass was determined by calculation from direct counts using the mean-cell-volume method (Nauwerck 1963).

A preliminary assessment of grazing rates was made to determine the possible fate of phytoplankton primary production and to aid in assessing the lake or pond food potential. Estimates were based on the relationship between the daily primary production and the calculated phytoplankton renewal rates.

It was not possible to make calorimetric measurements of the components of the aquatic communities at this time. However, the values for the algal and copepod components are probably very similar (cf. Cummins and Wuycheck 1971) and would not change calculated efficiency rates appreciably. Although it was not possible to measure assimilation rates ($K_1$ or ecological efficiency) directly for fish, the food intake rates suggested for Lake Sevan trout (Winberg 1971, p. 134) are close to those noted in other studies in oligotrophic mountain lakes. It is unlikely that the $K_1$ is any higher than 8 per cent on the basis of freshweight, or 16 per cent on the basis of caloric content. Caloric values for salmonid freshweight are approximately twice those for dipteran larvae, according to Cummins and Wuycheck (1971).

## RESULTS

The experimentally determined phytoplankton primary production for 1967 in Snowflake Lake was 76.4 kg C $ha^{-1}$ $yr^{-1}$. Accepting 10 per cent of freshweight as carbon (Nauwerck 1963), this is equivalent to 764 kg frwt $ha^{-1}$ $yr^{-1}$. Using Platt and Irwin's (1973) conversion factor, annual phytoplankton production is equivalent to 87 kcal $m^{-2}$, close to some low-productivity, oligotrophic lakes in North Karelia (Alimov and Winberg 1972). Annual phytoplankton production for Teardrop Pond was determined at 82.8 kg C $ha^{-1}$ $yr^{-1}$, or 828 kg frwt $ha^{-1}$ $yr^{-1}$, approximately equivalent to 94.3 kcal $m^{-2}$ $yr^{-1}$. Although no measurements of macrophyte or periphyton production have been made, it is estimated that inclusion of this production would give a gross primary production less than 1.5 times the measured phytoplankton primary production. Because there are no macrophytes in Snowflake Lake, it is expected that periphyton production would increase gross production by no more than 1.25 times in that lake.

The maximum *D. tyrrelli* biomass for Snowflake Lake was 52.7 kg $ha^{-1}$; mortality was calculated to be 16 per cent (Anderson 1972). The maximum biomass for *D. tyrrelli* in Teardrop Pond was 32.4 kg $ha^{-1}$ (second generation), and the biomass for each of the populations of *D. shoshone* and *E. intricatus* was approximately equivalent to *D. tyrrelli* second generation. Experiments and observations (Anderson 1967, 1970*b*) indicated that *D. shoshone* copepodids III to VI preyed heavily on the first generation of *D. tyrrelli*, but that much of the food for the predaceous copepods came from other sources. Mortality of the first generation of *D. tyrrelli* was assessed to be 85 per cent, and of the second 15 per cent (1969 data).

Table 2 is a summary of representative data on grazing-rate determinations. On the basis of the percentage of the copepod body weight consumed per day times the lifespan, if assessed grazing rates were representative for the species and other data were consistent, then Snowflake Lake copepods ate 16.1 times their biomass per year and Teardrop Pond copepods ate 15.8 times their biomass per year, and the $K_1$ or ecological efficiencies were 6.2 per cent for the former and 6.35 per cent for the latter.

Table 3 is a summary of phytoplankton primary production, zooplankton biomass and production, benthic biomass, generation times and production (some benthic data need further substantiation).

In 1966 and 1967, fishermen's catches included many large fish (up to 45 cm), but rather thin fish ranging from 22 cm to 28 cm appear to have dominated catches from 1968 to 1971. Gill net catches in 1973 indicated that the fish population had diminished considerably since 1966 when the lake was last stocked. Only 23 fish were caught in two 15-hour sets with 100 m of gill nets of various meshes. The condition of the fish had improved; all but one were between 28 cm and 33 cm in length and all were much larger in girth than in 1967. Stomach contents in 1967 contained 40 per cent by volume terrestrial insects and other organisms and 60 per cent aquatic organisms, whereas stomach contents in 1968 yielded 20 per cent terrestrial organisms and 80 per cent aquatic organisms. Most fish stomachs were comparatively empty in 1967 through 1968. Analyses of 1973 stomachs have not been completed. Benthic samples collected in 1967 yielded extremely few invertebrates, and those were very small ($< 4$ mm). Samples collected in 1973 indicated a substantial increase in biomass and the presence of many large dipteran larvae (up to 22 mm).

## DISCUSSION

On the basis of the limnological features of the two waters and their phytoplankton primary production estimates, it is likely that zooplankton production and biomass were near the maxima which could be expected, and that some food must come from sources other than phytoplankton production. Because of the slow growth rates for the crustacean zooplankters in these lakes, the differences between the $P/B$ ratios for the zooplankton populations and the benthic communities are much lower than the 3- to 7-fold differences indicated for some lakes in the USSR (Alimov and Winberg 1972, Winberg 1970). Phytoplankton production figures and projected secondary production figures (calculated as though both waters contained fish) sup-

TABLE 2

*Grazing by Diaptomus tyrrelli*[a] *in Snowflake Lake and Teardrop Pond relative to phytoplankton renewal rates*

| Location and date | Mean[b] phyto-biomass mg frwt $m^{-3}$ | Calculated[b] phyto. renewal coefficient[d] | Biomass change, dawn to sunset | Biomass[b] grazed, calculated | Copepod[a] numbers $m^{-3}$ | Biomass grazed copepod$^{-1}$ (mg) | Mean[c] copepod body wt (mg) | % copepod body wt grazed per day |
|---|---|---|---|---|---|---|---|---|
| Teardrop Pond August 1969 | 47 | 21.2 | ×2 | 949 | $9.0 \times 10^4$ | 0.0105 | 0.060 | 18 |
| Teardrop Pond May 1970 | 61 | 13.2 | ×2 | 744 | $12.5 \times 10^4$ | 0.0059 | 0.035 | 17 |
| Snowflake Lake July 1967 | 47 | 1.89 | ×1 | 89 | $1.25 \times 10^4$ | 0.0071 | 0.025 | 28 |
| Snowflake Lake August 1967 | 15 | 3.00 | ×1 | 45 | $1.15 \times 10^4$ | 0.0039 | 0.053 | 7 |
| Snowflake Lake August 1969 | 87 | 0.64 | ×1 | 56 | $2.0 \times 10^4$ | 0.0028 | 0.040 | 7 |

[a] Dominant crustacean plankter $\geq 90\%$ total crustacean numbers; *D. tyrrelli* in both waters.
[b] For upper 8 m in Snowflake Lake.
[c] Calculated value (unpublished data).
[d] Activity-coefficient ×10 (Nauwerck 1963).

TABLE 3

*Summary of phytoplankton primary production, zooplankton biomass and production, and generation times*

| Location | Annual* phyto. production | Zooplankton* ecolog. efficiency | Zooplankton* prod. from phyto. (calc.) | Zooplankton* prod. other sources (est.) | Zooplankton* biomass (max. meas.) | Zoopl. $P/B$ (est. min.) | Zooplankton gen. per year | Benthos* biomass (max. meas.) | Benthos $P/B$ (est. min.) | Benthos gen. per year |
|---|---|---|---|---|---|---|---|---|---|---|
| Snowflake Lake | 764 | 6.2 | 47.4 | 16 | 52.7 | 1.2[a] | 1 | 87 | 0.85[d] | 0.5 |
| Teardrop Pond | 828 | 6.35 | 52.5 | 45 | 32.4[b] | 3.0[c] | 2 | 177 | 1.5[e] | 1 |

* kg frwt $ha^{-1}$.
[a] Estimate on basis of 16% mortality up to copepodid VI (Anderson 1972) and estimates of production from other sources (1967 data).
[b] Second generation only: 2nd generation mortality estimated at 15%; 1st generation estimated to be 85% (1969 data).
[c] Estimated on basis of combined mortality of 50% and estimates of production from other sources.
[d] $P/B$ estimate based on mean generation time of 2 years for benthic organisms in Snowflake Lake.
[e] $P/B$ estimate based on mean generation time of 1 year for benthic organisms in Teardrop Pond.

port the conclusion of Brylinski and Mann (1973) that the production per unit surface area will be very similar from morphometrically different waters which are alike in most other limnological characteristics.

The small percentage of organic matter in the bottom sediments of the two waters indicates a high overall trophic efficiency and a high rate of nutrient turnover. The small input of nutrients into the lakes coupled with the export of nutrients through fish production could contribute to a gradual decline in production, especially in Teardrop Pond.

The maximum fish production which could be expected from either of the two waters would be less than that theoretically possible from the complete consumption of the invertebrate biomass ($H_m$; Table 4).

In calculating this maximum, even organisms known to be too small to serve as food for trout (except perhaps fingerlings) were included. The probability that about 30 per cent of the fish diet may come from outside the lake ecosystem was also taken into account. Reed and Bear (1966) found that this contribution may be even higher in alpine streams. The optimum expected fish production was calculated on the basis of 'available' food and $P/B$ estimates for the food organisms, not simply on standing-crop biomass of food-organisms. In sport-fisherman's language, the projected optimum annual yield from Snowflake Lake would be equivalent to fifty-five 450-g (one-pound) fish or one-hundred-ten 225-g (half-pound) fish, and it is expected that the yield from Teardrop Pond would drop from the equivalent of about fifty-five 225-g fish in the first year to a long-term yield of 9 or 10 if the pond was stocked annually (Table 4). The projected decline after the first year is based on the expectation that large invertebrate species would be eliminated rapidly in the first year (cf. Anderson 1972) and that standing-crop biomass and production would be similar to Snowflake Lake per unit surface area after the first year.

The production levels calculated for these two waters seem rather low, but are realistic compared to production figures for more eutrophic European mountain lakes (Grimaldi and Nűmann 1972, Roth and Geiger 1972). Ryder and Johnson (1972) estimated the maximum allowable annual yield of piscivorous *Salvelinus namaycush* from a small, oligotrophic lake in Ontario to be between 0.25 and 0.5 kg/ha, limits comparable to those assessed for non-piscivorous trout in Snowflake Lake and Teardrop Pond. These authors noted that it is not uncommon for 2 or 3 years' accumulated production to be removed in one day's sport fishing in such lakes.

Indications of recovery of the benthic community in Snowflake Lake with the decline in fish numbers is evidence that optimum production levels are easily exceeded and that over-exploited food-organism populations are slow to recover in alpine lakes. The improved condition of the individual fish in 1973 is another indication that optimum production is more likely to occur with fewer fish in such oligotrophic lakes.

## CONCLUSIONS

Whereas numbers of fish stocked have sometimes been based on expected survival rates as low as 1.5 to 6 per cent (e.g. Mottley 1939), it is expected here that at least 60 per cent of fingerlings stocked in oligotrophic alpine

TABLE 4

*Projection of maximum and optimum sport-fish production*[a] *from Snowflake Lake assessed from P/B ratios and*

| | $H_m$ | | | | |
|---|---|---|---|---|---|
| | Zooplankton | Benthic fauna | Factor[c] | Total kg/ha | Total kg/lake |
| Snowflake Lake | 4.2 | 7.0 | ×1.43 | 16.0 | 114.0 |
| Teardrop Pond 1st year | 7.8[d] | 14.2 | ×1.43 | 31.4 | 12.6 |
| Teardrop Pond 2nd year | 5.2 (?) | 7.0 (?) | ×1.43 | 14.7 | 7.0 |

[a] Using an ecological efficiency of 8% based on freshweights.
[b] Assuming that the total maximum invertebrate biomass would be available to the fish.

waters could survive and grow to a catchable size. Such a survival rate could be expected because of improvements in methods of fish transfer (e.g. Nelson 1968, Ward and Cuerrier 1967), because cannibalism would be minimal in a situation where the fish population was numerically small, and because predation by other animals (e.g. loons, dragonfly naiads) is infrequent or non-existent in these high lakes.

Table 5 summarizes the stocking levels suggested for optimum production, based on a survival rate of 60 per cent and on the expectation that annual production would be regularly removed. Although a 225-g fish is perhaps less desirable than 2-kg 'lunkers' from the sport-fisherman's standpoint, the smaller fish is less cannibalistic, requires less of its food intake for maintenance, and has a greater relative growth in the first two years. A few of these smaller fish will undoubtedly escape capture in Snowflake Lake, resulting in a more balanced population capable of using the food resource more efficiently (cf. Rawson 1947). The maximum numbers given in Table 5 are based on the possibility of utilization of the entire standing crop in one

TABLE 5

*Summary of projected annual stocking levels*[a] *for optimum utilization of fish-food potential, and projected fish yields*

| | Stocking (fingerlings) | | | | Projected yield as 225 g fish per lake | |
|---|---|---|---|---|---|---|
| | Maximum (1 year) | | Optimum (long-term) | | Maximum, 1 year only | Optimum, long term |
| | No./ha | No./lake | No./ha | No./lake | | |
| Snowflake Lake | 115 | 835 | 25 | 185 | 500 | 110 |
| Teardrop Pond | | | | | | |
| 1st year | 230 | 90 | (130?) | (50?) | 55 | — |
| long term | (130?) | (50?) | 35 | 15 | — | 10 |

[a] Expected maximum mortality of 40% between hatchery and harvest, and assuming that the annual fish production is harvested.

*and Teardrop Pond, based on total food present ($H_m$)[b] or on 'available' production ($H_0$) standing-crop biomass determinations*

| | $H_0$ | | | | |
|---|---|---|---|---|---|
| | Zooplankton | Benthic fauna | Factor[c] | Total kg/ha | Total kg/lake |
| Snowflake Lake | 0 | 2.4 | ×1.43 | 3.5 | 25.0 |
| Teardrop Pond 1st year | 5.2 | 7.1 | ×1.43 | 17.6 | 7.0 |
| Teardrop Pond 2nd year | 0 | 3.5 (?) | ×1.43 | 5.0 | 2.0 |

[c] Based on 1967–1968 data, up to 30% of food organisms eaten may originate outside the lake.
[d] 1st-year total estimated at 3 times maximum biomass of *D. tyrrelli* (includes *D. shoshone* and *E. intricatus*).

year, a situation which would cause a sharp drop in production thereafter. Higher fish populations would contribute to lower fingerling survival because of both predation on fingerlings and decimation of food organisms. Lower growth rates and poorer condition in the fish would be the result.

Because Teardrop Pond freezes to the bottom each year, only a put-and-take fishery would be possible. Furthermore, to expect maximum growth to 225 g in one season may reflect undue optimism. At expected yields of 10 to 55 fish (legal daily limit for 1 to 5 fishermen in Alberta), it is questionable whether stocking is worth the effort and expense. The pond is probably more valuable as a study site. Too rarely have lakes been thoroughly investigated before being stocked for the first time, either for the assessment of production potential or for determinations of the impact of fish on the natural communities.

The standing crop of crustacean plankton seems to be an indicator of the fish-food potential, even though the plankton may not be utilized directly to any great extent in many alpine lakes with stable fish populations. Annual primary production also seems to be a useful indicator of sport-fish production potential in alpine waters, whether fish are present or not. It seems likely that production per hectare will be fairly constant for morphometrically different alpine waters as long as other limnological conditions are similar.

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*Acknowledgments.* Thanks are due to several people who have helped in the field and in other ways over many years, especially D. A. Blood, A. Colbeck, J. Kilistoff, and D. Krochak. I am especially indebted to Mr. J.-P. Cuerrier who foresaw the need for fundamental studies as a basis for long-range planning and who gave much encouragement in the initial phases of this study. Laboratory space was provided by the Biology Department of the University of Calgary. Most financial support was provided by the Canadian Wildlife Service and the National and Historic Parks Branch.

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*Symp. Biol. Hung.*, *15*, pp. 215–224 (1975)

# THE BIOMASS OF ZOOPLANKTON IN LAKE BALATON

by

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A number of data is available on the qualitative composition of zooplankton. Since the investigations carried out by Daday (1884, 1897) and France (1894) at the turn of the century the works of Náday (1914), Entz, jr. (1903, 1908, 1927), Entz et al. (1937), Sebestyén (1931, 1933, 1953, 1955, 1958, 1959, 1960, 1964), Sebestyén et al. (1951), Varga (1932, 1939, 1941) and recently the works of Ponyi (1965*a*, *b*, 1967, 1968), Ponyi and Zánkai (1972), Ponyi et al. (1968), P.-Zánkai and Kertész (1967) and P.-Zánkai and Ponyi (1970, 1971, 1972, 1973) are especially important.

We have far less information on the quantitative changes of zooplankton from the years preceding 1965. The majority of data are concerned with the open water in front of the Biological Research Institute of the Hungarian Academy of Sciences (Entz et al. 1937, Sebestyén 1953, 1955, 1958, Sebestyén et al. 1951). The first study by Sebestyén dealing with the quantitative changes of far-off areas of the lake was only published in 1960.

The biomass data obtained so far in connection with Lake Balaton refer exclusively to plankton living in the area in front of the Institute.

The recognized investigation of Lake Balaton started in 1965 planned to continuously detect the quantitative and qualitative trend of zooplankton mass referring to the whole lake. The horizontal distribution of the members of the zooplankton was the main issue to be investigated, the vertical distribution being not so significant on account of the shallow water of Lake Balaton.

This lecture is concerned with some important conclusions drawn from the results of the investigations carried out in 1965 to 1967 on the most significant animal groups (Rotatoria and Crustacea) from the point of view of biomass.

## COLLECTING PLACES AND METHODS

Samples were collected for five months in 1965, for seven months in 1966, and for six months in 1967 at 1 (in 1965) and 3 points (in 1966–67), of each of the five transversal sections of the lake (M, K, G, A, E; Fig. 1). The monthly collection of the samples was made within two days in order to make a comparison between the far-off sections, too.

The Rotifera samples were taken with the help of the Friedinger apparatus from depths of 0.3, 1, 2, 3 and, when possible, from 4 metres. The one-litre water samples taken from different depths were poured together in

order to obtain more reliable average values for estimation, subsequently, the mixture was preserved with formalin; after sedimentation the surplus water was removed by the Hentschel method (Entz 1937). After having determined the volume of the condensed samples, one-third and one-fourth of them was examined, of which amounts of 1, 2 or 4 ml of sample were pipetted in each case into a $60 \times 30$ mm counting dish, then in turn each sample was counted under a magnification of $\times 130$. This procedure depending on the good parallels was repeated 3–6 times.

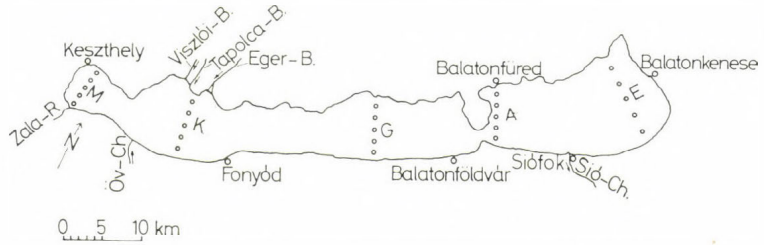


Fig. 1. Collecting places in Lake Balaton (for explanation of symbols see text)

The Crustacea collections were performed by means of a water-column-scooping-filtering apparatus devised by Sebestyén (1960). The apparatus was lifted three times from the bottom to the surface and the filtrate obtained according to the depth of water at the places of sampling (3 m on an average) ranged between 86–125 litre. After repeated shaking of the samples aliquots containing at least 1,000 specimens were taken from each sample for examination. Depending on the density of the individuals, portions of 1/3–1/6 of the samples were put into the counting vessel.

The volume-values of Rotatoria biomass determined by Sebestyén (1958) were used for calculation, namely those of the 'forms of warm water' according to the possibilities, since the samples had been collected from May to November every year. The specific weight of the animals was taken as a unit, the biomass being expressed in $\mu$g wet weight per litre.

The biomass of crustaceans had to be determined partly directly on the basis of dry weight. Where being impossible, e.g. in case of their larvae, it was estimated according to Sebestyén (1955) and Hall et al. (1970).

## RESULTS

Among the most frequent rotifers of the lake (7 species) *Polyarthra vulgaris*, *Keratella quadrata* and *Pompholyx sulcata* represent the highest biomass values.

On the basis of the average biomasses of three years, *Polyarthra vulgaris* is of the greatest importance showing a value of 8.3 in the Keszthely Bay and in its surroundings and 16.0 $\mu$g per litre in the other parts of the lake. *Keratella quadrata* and *Pompholyx sulcata* display different distribution of biomass in the two areas: the former occurred in 7.9 $\mu$g per litre in the samples taken from the Keszthely Bay and from its surroundings (segments M, K), the latter in 0.4 $\mu$g per litre. In the segments representing about two-thirds

TABLE 1

*Quantitative distribution of the most frequent rotifers along five transversal sections of lake Balaton (μg/l, biomass)*

| Date | Collecting place | | | | | |
|---|---|---|---|---|---|---|
| | M + K | G + A + E | M + K | G + A + E | M + K | G + A + E |
| | *Polyarthra vulgaris* | | *Keratella quadrata* | | *Pompholyx sulcata* | |
| 1965 June | 0.4 | 1.3 | 0.3 | 0.9 | 0 | 2.3 |
| July | 0 | 0 | 2.2 | 0.7 | 0 | 20.8 |
| August | 0 | 0 | 11.9 | 0 | 0 | 11.0 |
| September | 18.8 | 13.7 | 5.0 | 0.8 | 0 | 11.9 |
| October | 18.8 | 65.9 | 0.3 | 0.7 | 0 | 3.9 |
| average | 7.6 | 16.2 | 3.9 | 0.7 | 0 | 9.9 |
| 1966 May | 7.7 | 35.2 | 1.1 | 3.0 | 0.1 | 14.6 |
| June | 9.1 | 2.2 | 33.5 | 1.3 | 5.3 | 17.4 |
| July | 1.2 | 11.1 | 11.0 | 1.3 | 0.2 | 16.8 |
| August | 3.6 | 21.0 | 17.0 | 2.7 | 0 | 20.1 |
| September | 13.8 | 9.9 | 15.9 | 1.5 | 0 | 5.3 |
| October | 29.0 | 43.2 | 11.0 | 4.9 | 0 | 2.3 |
| November | 2.4 | 7.3 | 0.5 | 2.8 | 0 | 0.2 |
| average | 9.5 | 18.5 | 12.8 | 2.5 | 0.8 | 10.9 |
| 1967 May | 8.8 | 11.1 | 13.9 | 37.7 | 0.9 | 7.8 |
| June | 11.9 | 6.9 | 5.9 | 2.0 | 0.6 | 11.2 |
| July | 1.1 | 8.5 | 6.3 | 2.8 | 0.5 | 21.4 |
| August | 3.4 | 24.5 | 11.9 | 1.6 | 0 | 9.4 |
| September | 2.2 | 11.9 | 4.2 | 0.3 | 0 | 5.5 |
| October | 19.7 | 16.6 | 0.3 | 1.5 | 0 | 4.4 |
| average | 7.8 | 13.2 | 7.1 | 7.6 | 0.3 | 9.9 |
| average of 3 years | 8.3 | 16.0 | 7.9 | 3.4 | 0.4 | 16.2 |

of the lake (segments G, A, E), the former (i.e. *Keratella quadrata*) showed 3.5, while the latter (i.e. *Pompholyx sulcata*) 10.3 μg per litre biomass value (Table 1).

The changes of the total Rotatoria biomass can be seen in Fig. 2, next to the biomass-values of rotifers those of the carnivorous crustaceans (*Mesocyclops leuckarti, Cyclops vicinus, Acanthocyclops vernalis, Leptodora kindtii*) are shown. The changes of the Rotatoria biomass are not always connected with those of the carnivorous Crustacea (e.g. in a few months in 1967).

But if the average biomass of Rotatoria and carnivorous Crustacea are compared in a three-year period in two different areas of the lake, it will be seen that their biomass values are in inverse ratio to each other. In the M + K area the average biomass of carnivorous crustaceans is 41 μg per litre (*Mesocyclops* totals 9 μg per litre of this value), that of Rotatoria 24 μg per litre. In the G + A + E area the average biomass of Rotatoria is 42 μg per litre, and that of the Crustacea is only 26 μg per litre (*Mesocy-*

*clops* totals 7 μg per litre). Thus it can be supposed that the course of the different distribution of the dominant Rotatoria species is determined by the feeding activities of carnivorous Crustacea (Fig. 2).

Systematic quantitative investigations of the Rotatoria plankton involved only the open water area in front of the Biological Institute (segment A) before 1965. The total biomass of Rotatoria continuously increased up to

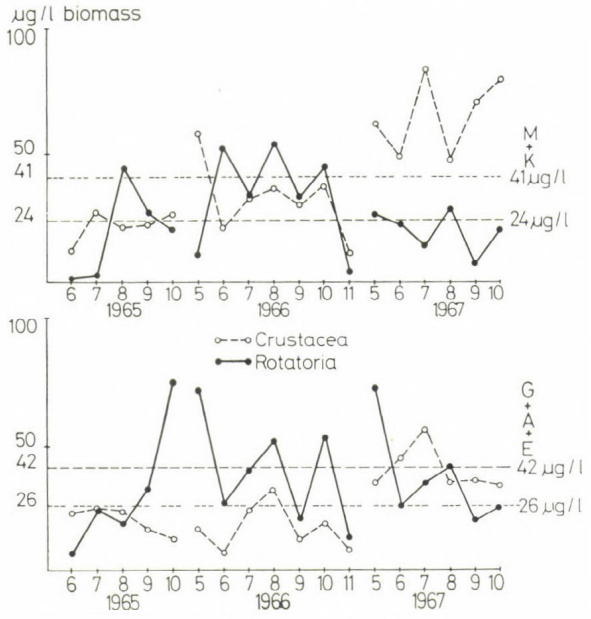


Fig. 2. Changes in the total biomass of Rotatoria and carnivorous crustaceans in two areas of Lake Balaton

1951 in segment A (Table 2). Since then a stagnation occurred instead of a further increase, the reason of which is unknown.

Among planktonic Crustacea (9 species) in Lake Balaton, with regard to biomass value, *Eudiaptomus gracilis*, *Cyclops vicinus*, *Diaphanosoma brachyurum*, *Mesocyclops leuckarti*, *Daphnia cucullata* are of the greatest importance.

The distribution of all biomass of planktonic Crustacea similarly to Rotatoria was different in the two areas of the lake. While in the area marked with M + K, average biomass in a three-year period was 91–109 μg per litre, in the other areas it is 66–75 μg per litre. This phenomenon can be connected with the distribution of algal quantity. As it can be seen in Fig. 3, the algal quantity in segments M + K is more than at any other place. The monthly changes of crustacean biomass in the segments are in some cases in accordance with changes in the number of individuals of algae (e.g. in 1965, in sections E, A and G; and in 1966 in sections E and A), while in other cases they are not. It can be supposed to be due, especially in the M + K area, to the increasing number of Cyanophyta (*Aphanizomenon flos-aquae* var. *klebahnii*).

TABLE 2

*Quantitative changes of total planktonic Crustacea and Rotatoria in the waters in front of the Biological Research Institute (transversal section 'A')*

| Time of examination | | Crustacea ind./l average value | Rotatoria µg/l biomass |
|---|---|---|---|
| Year | Month | | |
| 1936 | May–June | 25.6 | 6.5 |
| 1937 | May–November | 35.1 | 8.7 |
| 1938 | May–November | 43.5 | 12.1 |
| 1947 | May–November | 46.4 | 29.0 |
| 1949 | May–November | 50.9 | 8.4 |
| 1951 | May–November | 83.2 | 40.9 |
| 1955 | July–August | 49.7 | — |
| 1956 | June | 19.4 | — |
| 1958 | June | 17.0 | — |
| 1965 | June–November | 12.4 | 22.4 |
| 1966 | May–November | 12.9 | 42.0 |
| 1967 | May–October | 20.4 | 35.5 |

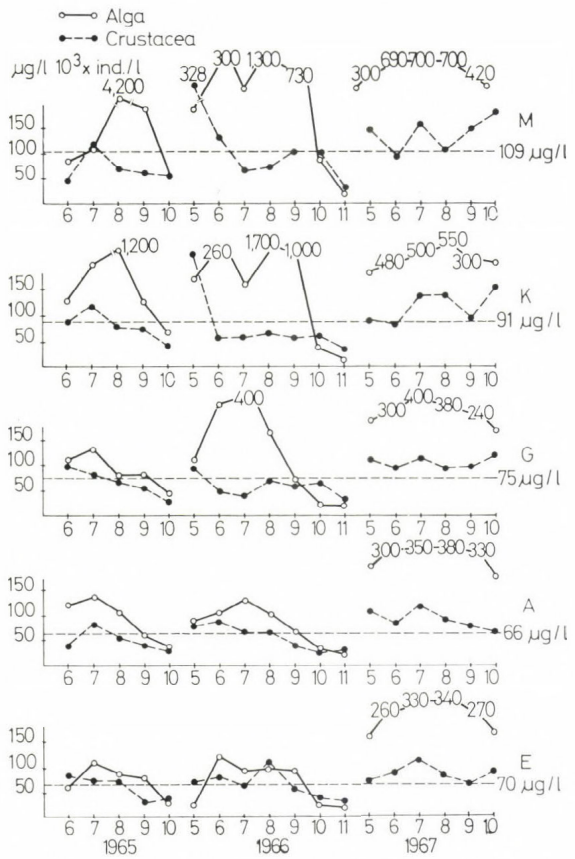


Fig. 3. Changes in total biomass of planktonic Crustacea and in the total number of algae

Figures 4 and 5 may indirectly support these hypotheses indicating the quantitative proportions of filter-feeding and carnivorous crustaceans, those of Cyanophyta and other algae in the sections investigated at the same time. In May 1966, Cyanophyta was small in number and the number of individuals of other algae gradually decreased from section M to section E,

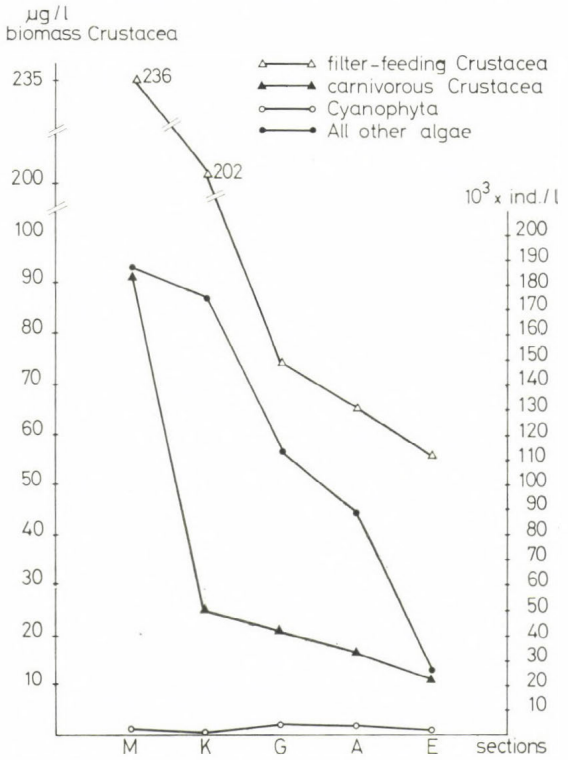


Fig. 4. Changes in planktonic Crustacea and in the total number of algae, in five sections of Lake Balaton in May 1966

thus the biomass of filter-feeding and predatory Crustacea also decreased (Fig. 4). In the summer of 1966, in sections M and K water-bloom of *Aphanizomenon* occurred. In the areas where the number of Cyanophyta was high the biomass of filter-feeding crustaceans, in comparison with the other areas, was significantly less (Fig. 5).

Figure 6 shows the one-year horizontal change of the average biomass of filter-feeding and carnivorous crustaceans. While in 1965 the biomass of predatory crustaceans was about 20 µg per litre, that of the filter-feeding crustaceans was the treble of it. In 1966, apart from section M, the situation was nearly the same. In the subsequent year the biomass of carnivorous crustaceans, especially of species of *Cyclops*, significantly increased and amounted to the order of magnitude of the biomass of filter-feeding crustaceans, i.e. significant changes took place in the trophic interrelations of plankton association.

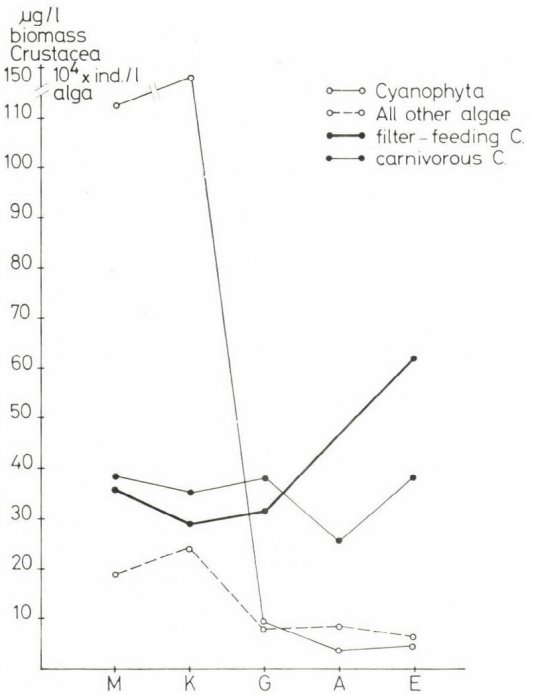


Fig. 5. Changes in planktonic Crustacea and in the total number of algae, in five sections of Lake Balaton, in August 1966

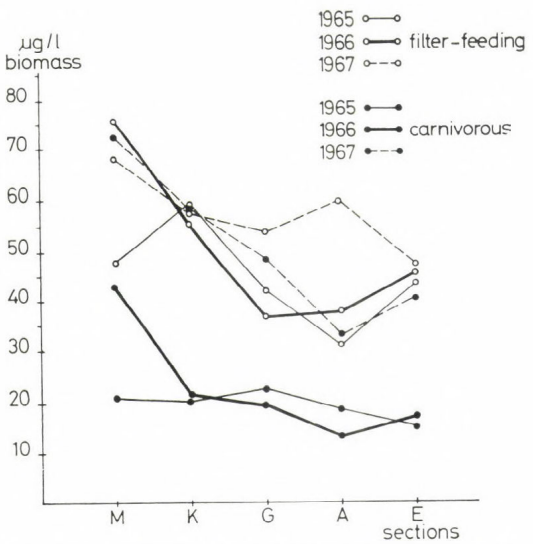


Fig. 6. Average biomass distribution of planktonic crustaceans in five sections of Lake Balaton

TABLE 3

*Average quantitative distribution of more important planktonic groups and some other components in two areas of Lake Balaton*

| | M + K | G + A + E | Date | References |
|---|---|---|---|---|
| Organic carbon content mg/l | 6.42 | 5.36 | July 1966 | Felföldy et al. 1970 |
| Chemical $O_2$-consumption | 4.9 | 3.8 | July 1966 | Felföldy et al. 1970 |
| Total-P (mg/m$^3$) | 86.6 | 51.5 | April–December 1969 January–February 1970 | VITUKI 1972 |
| Bacteria ($10^5$ cells/ml) | 4.7 | 3.5 | May–November 1966 to 1970 | Oláh, 1971 |
| Alga ($10^5$ ind./l) | 4.9 | 1.4 | May–November 1965 to 1967 | Tamás 1967–1969 |
| Rotatoria ($\mu$g/l biomass, fresh) | 24 | 42 | May–November 1965 to 1967 | P.-Zánkai and Ponyi 1973 |
| Filter-feeding Crustacea ($\mu$g/l biomass, dry weight) | 60 | 44 | May–November 1965 to 1967 | Ponyi and N.-Horváth 1973 |
| Carnivorous Crustacea ($\mu$g/l biomass, dry weight) | 39 | 25 | May–November 1965 to 1967 | Pony and N.-Horváth 1973 |

Former and present data concerning the number of individuals of crustaceans collected in identical periods in the area in front of the Biological Research Institute can be compared (Table 2). It was observed that the number of crustaceans had been gradually increasing from 1936 up to 1951, with a decrease since then. In lack of data, conclusions on the whole Lake Balaton cannot be drawn from this instance.

## DISCUSSION AND SUMMARY

Results referring to the biomass of Rotatoria and planktonic Crustacea can be summarized with the help of Table 3 as follows:

A great number of inflows running into Lake Balaton get into sections M and K resulting in their degree of supply in nutrient being higher than in other areas of the lake. Consequently, the quantity of algae in this area is significantly larger than elsewhere. This nutrient basis promotes existence of filter-feeding crustaceans in great quantities leading to an increase in population density. For the inverse proportion of biomass value of planktonic rotifers and predatory crustaceans in the two areas differing in water quality, the predatory crustaceans seem to be responsible.

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*Symp. Biol. Hung.*, *15*, pp. 225–231 (1975)

# QUANTITATIVE UNTERSUCHUNGEN ZUR NAHRUNGSAUSNUTZUNG DURCH *EUDIAPTOMUS GRACILIS*

von

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Die Ernährungsbiologie von *Eudiaptomus gracilis* wurde schon früher untersucht. Als erste haben sich im Jahre 1961 Malowitskaja und Sorokin mit der Nahrungsausnutzung dieser Art beschäftigt. Sie haben die $^{14}C$-Isotopenmethode angewendet; als Nahrung dienten Scenedesmus, Aphanizomenon, Melosira und Asterionella. Im Jahre 1971 prüfte Schindler die Ernährung von *Eudiaptomus* mit 11 verschiedenen Algen. Gleichzeitig wurde der Energiehaushalt und Populationsdynamismus dieser Krebsart von Kibby eingehend untersucht. Da die beiden Forscher unterschiedliche Zielsetzungen hatten und unterschiedliche Methoden anwendeten, lassen sich ihre Ergebnisse nicht miteinander vergleichen.

Unser Ziel war die Untersuchung des Nahrungsspektrums von *Eudiaptomus gracilis*, der im Balaton das ganze Jahr hindurch in dominanter Menge lebt. Außerdem wollten wir die optimale Nahrungskonzentration bestimmen.

Die Versuche wurden vom Mai 1972 durchgeführt, u. zw. im Sommer nur im Laboratorium, im Winter sowohl im Laboratorium als auch unter natürlichen Umständen, wie im folgenden ausgeführt wird.

Die als Nahrung verwendeten reinen Algenstämme stammen aus der Algensammlung von E. Kol bzw. von L. Felföldy. Die Diatomenstämme wurden uns von Dr. Marvan aus Brno bzw. von Dr. Hindák aus Bratislava zur Verfügung gestellt, wofür wir an dieser Stelle herzlich danken. Die Algenstämme wurden einheitlich in der Stammlösung nach Knopp-Pringsheim gezüchtet und nachfolgend mit markiertem $NaH^{14}CO_3$ behandelt. Die Markierungen waren von verschiedener Dauer. Die Algen wurden dann durch ein Membranfilter (mit dem Porendurchmesser von 0,2 $\mu$) so lange filtriert und gewaschen, bis das Filtrat keine Aktivität mehr zeigte, und die gewaschenen Algen wurden sodann in filtriertem Balatonwasser suspendiert. Die Aktivität und der organische Kohlenstoffgehalt der auf diese Weise vorbereiteten Nahrung wurden vor jedem Versuch bestimmt.

In den Sommermonaten, wenn die Temperatur im Laboratorium mit der des Balatonwassers gleich oder die Abweichung gering war, wurden die Krebse 2–3 Stunden lang bei Laboratoriumstemperatur adaptiert. Im Winter betrug die Adaptationszeit 24 Stunden bis zu 6 Tagen, in Abhängigkeit vom Ziel des Versuches. Wurden die Versuche im See durchgeführt, kamen die Tiere aus dem Sammelgefäß nach Durchspülen mit filtriertem Balatonwasser sofort in die Versuchsgefäße.

Die Fütterung dauerte 2–22 Stunden (im Laboratorium 2–4, im See 20–22 Stunden). Die verhältnismäßig lange Expositionszeit war erforderlich, damit die Aktivität der Krebse entsprechend hoch sei. Wie nämlich

aus den Ergebnissen von Conover (1966) und Richman (1966) hervorgeht, ist der Zusammenhang zwischen der Assimilation und der Expositionsdauer des Versuches nicht signifikant. Die Untersuchungen wurden mit der Methode von Sorokin (1968) durchgeführt. Die Krebse erhielten zunächst markierte Nahrung, dann aber wurden sie 4 Stunden lang mit unmarkierten Algen gefüttert, damit ihr Darmkanal von den aktiven Stoffen befreit sei. Nachfolgend wurde die eingebaute Aktivität des Körpers bestimmt. Für die Auswertung der Ergebnisse diente der von Sorokin beschriebene Assimilationsindex, der das Verhältnis zwischen der in 24 Stunden eingebauten Nahrung und dem organischen Kohlenstoffgehalt des Körpers darstellt (Ca/C%).

Die Aktivität wurde mit der Szintillationseinrichtung für Flüssigkeiten USB.2 gemessen und der Wirkungsgrad der Bestimmung mit Hilfe eines inneren Standards (Toluol) festgestellt. Bei der Bestimmung der Aktivität der Algen wurde auf Grund der Ergebnisse von Ward und Nakanishi (1971) die Selbstabsorption unberücksichtigt gelassen. Die Selbstabsorption der ausgewachsenen Männchen und Weibchen von *Eudiaptomus gracilis* hingegen wurde mit Hilfe der Verbrennungsmethode von Gupta (1966) bestimmt. Der Wert des Selbstabsorptionskoeffizienten beträgt 1,38.

Der organische Kohlenstoffgehalt der Tiere und der Algen wurde durch nasse Verbrennung bestimmt (Ostapenja 1965). Bei den Tieren fand sich ein bedeutender Unterschied zwischen den in der Warmwasser- bzw. in der Kaltwasserperiode erhaltenen Werten. Zwischen dem 10. April und 16. November 1972 betrug der durchschnittliche organische Kohlenstoffgehalt von 2389 Tieren 2,804 $\mu$g, während 641 Tiere zwischen dem 19.

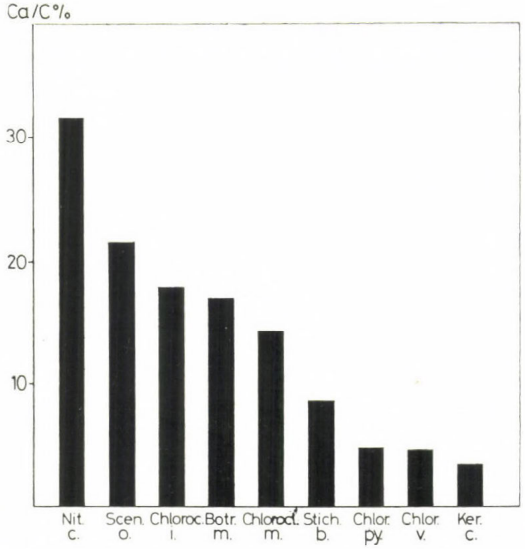


Abb. 1. Die Ausnutzung verschiedener Algennahrung, Nit. c. = *Nitzschia communis*, Scen. o. = *Scenedesmus obtusiusculus*, Chloroc. i. = *Chlorococcum infusionum*, Botr. m. = *Botrydiopsis minor*, Chlorocl. m. = *Chlorocloster minimus*, Stich. b. = *Stichococcus bacillaris*, Chlor. py. = *Chlorella pyrenoidosa*, Chlor. v. = *Chlorella vulgaris*, Ker. c. = *Keratococcus caudatus*

Januar und 10. April 1973 durchschnittlich 4,53 µg organischen Kohlenstoff erhielten.

In Abb. 1 ist die mit Algenarten durch *Eudiaptomus gracilis* erhaltene Assimilation dargestellt. Wie aus Abb. 1 hervorgeht, wurden am besten die zu den Kieselalgen gehörende *Nitzschia* und der zu den Chlorophyten gehörende *Scenedesmus* eingebaut, während der Einbau der 2 Chlorella-Arten und von *Keratococcus* der geringste war.

In den Versuchen wurden verschiedene Futterkonzentrationen verwendet, die jedoch alle höher waren, als dies zur maximalen Assimilation erforderlich ist.

Der Tabelle 1 ist zu entnehmen, daß die SD-Werte neben dem Assimilationsindex in einigen Fällen niedrig sind, z. B. bei *Botrydiopsis* (22. Aug.), in anderen Fällen sind sie aber hoch (*Keratococcus*, 31. Mai). In der Natur liegt der Grund hierfür wahrscheinlich in der ungewöhnlich hohen Algenkonzentration und evtl. im unterschiedlichen organischen Kohlenstoffgehalt der Versuchstiere. Letzterer ließ sich selbstverständlich nicht er-

TABELLE 1

*Die Ausnutzung verschiedener Algen durch Eudiaptomus gracilis*

| Algenarten | Datum | Temperatur des Balatonwassers °C | Anzahl der Proben | Ca/C% | Kohlenstoffgehalt des *Eudiaptomus* µg/C | Nahrungskonzentration mg C/l |
|---|---|---|---|---|---|---|
| *Keratococcus caudatus* | 29. 5. 1972 | 18,5 | 12 | 3,88±1,27 | 2,6 | 2,08–6,24 |
| | 31. 5. 1972 | 18.3 | 12 | 3,72±1,81 | 2,7 | 2,31–7,05 |
| | 5. 6. 1972 | 21,2 | 10 | 2,39±1,25 | 2,5 | 1,72–3,45 |
| *Chlorella pyrenoidosa* | 11. 6. 1972 | 22,5 | 10 | 3,23±1,34 | 2,6 | 2,26–5,09 |
| | 19. 6. 1972 | 22,2 | 11 | 5,78±2,84 | 2 6 | 1,95–5,19 |
| | 22. 6. 1972 | 23,5 | 10 | 4,97±2,19 | 2,9 | 1,66–4,99 |
| *Scenedesmus obtusiusculus* | 5. 7. 1972 | 21,0 | 11 | 21,60±5,05 | 2,9 | 1,76–5,29 |
| | 8. 8. 1972 | 22,5 | 10 | 22,00±3,39 | 2,9 | 1,61–4,83 |
| *Botrydiopsis minor* | 22. 8. 1972 | 16,0 | 11 | 16,63±1,86 | 2,7 | 1,93–5,82 |
| | 29. 8. 1972 | 18,5 | 8 | 17,33±4,14 | 2,7 | 1,43–5,70 |
| *Chlorocloster minimus* | 12. 9. 1972 | 16,8 | 9 | 12,34±2,91 | 2,7 | 1,34–6,03 |
| | 27. 9. 1972 | 14,0 | 8 | 15,92±3,10 | 2,7 | 1,10–5,50 |
| *Chlorococcum infusionum* | 17. 10. 1972 | 10,2 | 5 | 22,77±6,11 | 2,5 | 4,15 |
| | 23. 10. 1972 | 8,8 | 6 | 12,42±2,63 | 2,8 | 1,68–4,20 |
| | 2. 5. 1973 | 17,2 | 5 | 19,03±3,75 | 2,9 | 1,00 |
| *Stichococcus bacillaris* | 24. 10. 1972 | 8,8 | 6 | 8,21±1,46 | 2,8 | 2,88 |
| | 3. 11. 1972 | 10,2 | 6 | 8,32±4,30 | 2,8 | 3,36 |
| *Chlorella vulgaris* | 16. 11. 1972 | 8,3 | 11 | 4,43±1,35 | 2,6 | 2,65 |
| *Nitzschia communis* | 25. 7. 1973 | 21,5 | 3 | 32,75 | 3,7 | 0,54–1,09 |
| | 17. 7. 1973 | 20,0 | 3 | 35,56 | 3,2 | 0,47–0,93 |
| | 1. 8. 1973 | 21,5 | 4 | 27,50 | 3,2 | 0,47–1,40 |

mitteln. Die Standardabweichung beweist, daß bei der Erhöhung der Konzentration die Assimilation weder ab- noch zunimmt, sondern um einen konstanten Wert schwankt.

Der Zusammenhang zwischen der Konzentration des Futters und der Intensität der Assimilation wurde gleichfalls untersucht. Zu diesen Versuchen wurden 4 Algenarten verwendet: *Scenedesmus*, *Nitzschia*, *Chlorococcum* und *Botrydiopsis*. Die Versuche mit den beiden ersten Algen erfolgten im Sommer, mit den beiden letzteren im Winter.

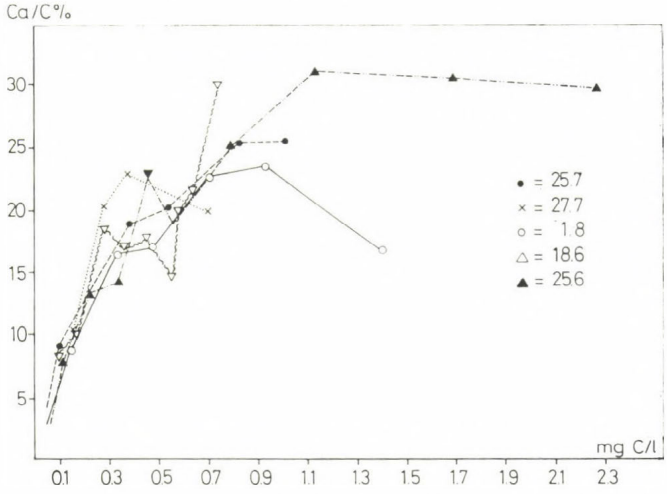


Abb. 2. Abhängigkeit der Nahrungsausnutzung von der Nahrungskonzentration in den Sommermonaten

Die optimale Nahrungskonzentration ist gemäß der Definition von Sorokin (1968): »Subsequent increase in the values of the concentration does not significantly increase the values of assimilation. Thus the latter concentration can be accepted as the lower end of the optimal range.«

In Abb. 2 sind fünf in der Sommerperiode durchgeführten Versuche dargestellt. Bei drei Versuchen dienten *Nitzschia*, bei zweien hingegen *Scenedesmus* als Nahrung. Der Assimilationsgrad nahm bis zur Konzentration von 0,27–0,45 mg Alge C/l in allen Versuchen rasch zu. Über dieser Konzentration wurden die Kurven flach und erreichten bei 0,7–1,1 mg Alge C/l die Sättigung.

Die mit *Chlorococcum* und *Botrydiopsis* im Winter durchgeführten Konzentrationsversuche (Abb. 3) veranschaulichen viel deutlicher als die im Sommer durchgeführten die Tatsache, daß die untere Grenze der optimalen Nahrungskonzentration 0,3–0,4 mg C/l beträgt. Sie zeigen ferner, daß die Standardabweichung sogar bei höheren Nahrungskonzentrationen im Winter bedeutend kleiner ist als im Sommer. Vergleicht man die im Sommer und im Winter erhaltenen Assimilationsdaten, so sieht man, daß die untere Grenze der optimalen Nahrungskonzentration im Winter niedriger ist als im Sommer. Ferner läßt sich feststellen, daß die obigen Werte in beiden Jahreszeiten höher sind als die entsprechenden Werte im Balaton. Aus den Daten

von Herodek und Tamás (1973) geht nämlich hervor, daß die Konzentration der Algenbiomasse im offenen See bei Tihany, woher die Tiere stammten, im Winter 0,5–1,0 mg/l beträgt, im Sommer hingegen sogar 4–5 mg erreichen kann. Die untere Grenze der Konzentration ist also 3- bis 5mal größer als die im offenen Wasser bestimmte Algenmenge.

Auch Malowitskaja und Sorokin (1961) haben den Zusammenhang zwischen Assimilation und Nahrungskonzentration bei *Eudiaptomus gracilis* untersucht, mit *Chlorococcum*-Algen als Nahrung. Sie sind der Meinung, daß » ...нормальная интенсивность питания диаптомусов наблюдается при величине биомассы водорослей 1 г/м³ и достигает оптимума при 4,84 г/м³.

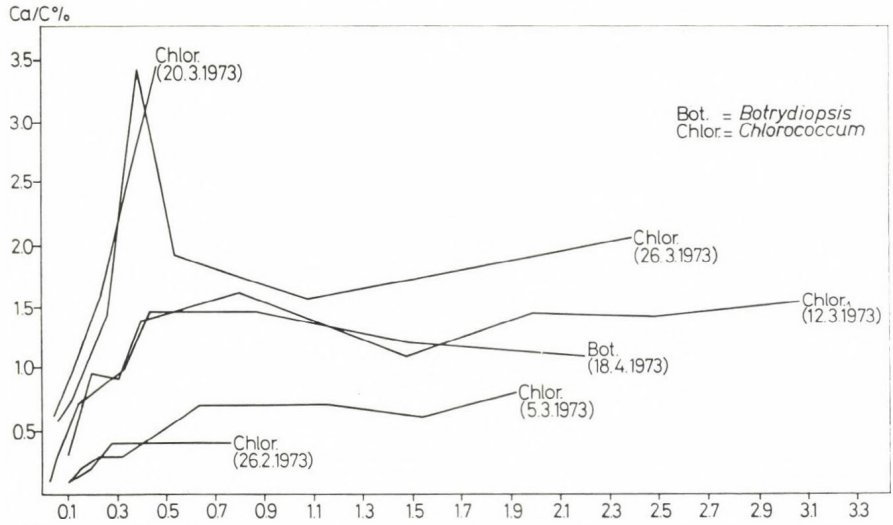


Abb. 3. Abhängigkeit der Nahrungsausnutzung von der Nahrungskonzentration zwischen 26. Februar und 18. April

Дальнейшее повышение концентрации корма оказывается малоэффективным.« Rechnet man diese Werte auf unsere C-Daten um, so folgt daraus, daß die Assimilation bis zu 0,48 mg C/l zunimmt. Unsere in der Kaltwasserperiode durchgeführten Versuche bestätigen die Daten der sowjetischen Verfasser.

Ferner wurde die Nahrungsausnutzung in den verschiedenen Jahreszeiten untersucht. Als Nahrung dienten *Chlorococcum*- und *Botrydiopsis*-Algen. Wie aus Abb. 4 hervorgeht, beträgt der Assimilationsindex von *Eudiaptomus* auf Grund der Versuche im Mai und Oktober 18 $\pm$ 4,12%. Als Nahrung diente *Chlorococcum*. Im Winter hingegen, wenn die Tiere nicht ins Laboratorium gebracht, sondern der Versuch wie oben beschrieben unter natürlichen Umständen durchgeführt wurde, betrug der Assimilationswert nur 1,58%. Nach einer 6 bzw. 4 Tage dauernden Adaptation unter Laboratoriumsbedingungen (22 °C) erhöhte sich der Index in geringem Maße (3,2%). Dieser Wert ist jedoch nur etwa ein Sechstel der im Oktober und Mai erhaltenen Werte. Die Versuche beweisen also, daß die Temperaturerhöhung

zwischen 4 und 22 °C auf die Assimilation von *Eudiaptomus gracilis* keine bedeutende Wirkung ausübt.

Der Unterschied zwischen der Assimilation im Sommer und im Winter kann nicht eindeutig erklärt werden.

1. Wir nehmen an, daß im Balaton zwei Populationen dieser Krebsart vorkommen. Im Sommer existiert eine Population mit sehr geringem Fettgehalt und niedrigem organischem Kohlenstoffgehalt, während die im Winter existierende Population einen hohen Fett- und Kohlenstoffgehalt besitzt.

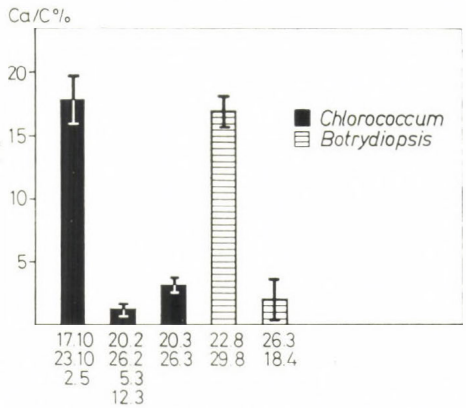


Abb. 4. Nahrungsausnutzung durch *Eudiaptomus* in verschiedenen Jahreszeiten

Angesichts des großen Fett- und Kohlenstolffvorrats zeigen diese Tiere keine große Freßlust in bezug auf die Algennahrung.

2. Infolge der niedrigen Temperatur filtrieren sie nur kleinere Wassermengen und da die Algenbiomasse nach Tamás im Winter nur 0,5–1,0 mg/l beträgt (also ein Drittel des Sommerwertes), nehmen sie unbedingt weniger Nahrung zu sich. Die Assimilation ist wahrscheinlich deshalb niedriger.

Nach der Adaptation nimmt der Filtrationsgrad und daher auch der Ernährungsgrad der Tiere zu, wie dies aus Literaturdaten hervorgeht. Eine 4- bis 6tägige Adaptation ist jedoch vermutlich zu kurz, die Tiere können ihre Fettvorräte nicht so schnell abgeben und dadurch zu einem besseren Appetit gelangen.

Kibby (1971) untersuchte die Ernährungsverhältnisse von *Eudiaptomus* bei unterschiedlichen Temperaturen und stellte fest, daß sich der Filtrationsgrad mit der Temperatur ändert. Der prozentuale Wert der Assimilation zeigte jedoch zwischen 5 und 20 °C keinen Unterschied, wenn *Chlorella*, *Scenedesmus*, *Diplosphaeria* oder *Ankistrodesmus* als Nahrung dienten.

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*Symp. Biol. Hung.*, *15*, pp. 233–245 (1975)

# DISTRIBUTION AND CHARACTERISTICS OF BACTERIA, PHYTOPLANKTON AND ZOOPLANKTON IN LAKE CASTORIA

by

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## INTRODUCTION

In autumn 1961, our hydrobiological researches were performed at Lake Castoria in Aegean Macedonia (Greece) in the frame of the scientific investigation of the Hydrobiological Institute at Ohrid.

The purpose of these investigations was to analyse the distribution and the characteristics of bacterioplankton, phytoplankton and zooplankton in this lake.

The present Lake Castoria is what is left of a much bigger and deeper lake which had a surface of 164 km$^2$ and depth of 50 m. Now the water surface is kidney-shaped and covers an area of 27.88 km$^2$ (Fig. 1). Maximum depth of the Lake is 10.4 m with an average depth of 3.56 m (Cvijić 1911). It is a eutrophic lake.

## MATERIAL AND METHODS

The material for these investigations was taken at one fixed station in the pelagial zone of the lake at a maximum depth of 8 m and from different layers (0, 1, 2, 3, 4, 5, 6 and 7 m).

The samples of lake water for bacterioplankton were collected with an aseptic modified ZoBell sampler (Ocevski 1966). The mud samples for the benthic bacterial communities were taken from the bottom with a Jenkin surface mud sampler (Mortimer 1941).

The phytoplankton samples were collected with Ruttner type water samplers, while the zooplankton with plankton nets No. 17.

The total number of bacteria was counted with the standardized procedure of the membrane filter method, using MF No. 2 (USSR) and with the help of a microscope their form, structure and volume were investigated.

The number of heterotrophic and anaerobic bacteria was counted by the plate counting procedure on mud extract media (Ocevski 1966).

The number and distribution of phytoplankton were studied by standardized

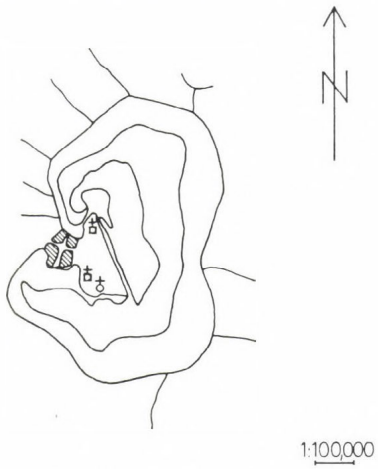


Fig. 1. Lake Castoria (Cvijić 1911)

procedures (Kozarov 1954, 1957). The maximum density of the phytoplankton population in the autumn of 1961 is represented by an average quantity of individuals in one ml of water.

For the determination of the spatial distribution of quantity and quality of zooplankton the standardized technique was applied (Serafimova-Hadžišče 1957). The density of the zooplankton population is represented by an average quantity of individuals in 1 $m^3$ of water.

At the same time some ecological conditions of the lake were measured as, e.g. transparence, temperature, pH, oxygen, $SiO_2$ and $HCO_3$.

## RESULTS

### *Ecological conditions*

The colour of the lake was brown. This phenomenon is attributed to the plankton algae *Ceratium hirundinella* (Stanković 1951). Transparence of the water, measured by Secchi disk, at 2 p.m. was 1.40 m. The temperature of lake water from the surface to the bottom ranged between 22 °C (in the surface layer) and 18 °C (at the bottom layer), demonstrating that in the water of Lake Castoria there were very slight temperature differences indicating temperature stratification.

The dissolved oxygen content and the presence of $HCO_3$ and $SiO_2$ in the lake water (Table 1) illustrate the slightly chemical stratification.

TABLE 1

*Temperature, pH, oxygen, $HCO_3$, $CO_2$ and $SiO_2$ at different depths in the water of Lake Castoria (30.9.1961)*

| Depth, m | temperature, °C | pH | Oxygen saturated, per cent | $HCO_3$, mg/l | $CO_2$, mg/l | $SiO_2$, mg/l |
|---|---|---|---|---|---|---|
| Surface | 22.00 | 8.8 | 156.48 | 144 | — | 1.5 |
| 1 | 21.00 | 8.6 | 150.48 | 146 | — | 1.8 |
| 2 | 20.50 | 8.5 | 103.81 | 147 | — | 2.2 |
| 3 | 19.50 | 8.5 | 28.49 | 147 | — | 1.7 |
| 4 | 19.00 | 8.1 | 65.04 | 147 | 2.505 | 1.8 |
| 5 | 18.00 | 7.7 | 56.87 | 147 | 3.132 | 1.65 |
| 6 | 18.00 | 7.7 | 15.67 | 147 | 3.132 | 1.8 |

The oxygen saturation amounted from 156.48 per cent (surface) to 15.67 per cent (at a depth of 6 m) of the normal values. At a depth of 3 m the absence of free $CO_2$ from the lake water was recorded. In the layers at depths of 4 to 6 m the free $CO_2$ content ranged from 2.505 to 3.132 ml per l of water. The pH ranged from 8.8 to 7.7 with a maximum at the surface.

### *Bacterioplankton*

In Lake Castoria the total number of microscopically determined bacterial plankton was rather high (Fig. 2). In the lake water the number of bacteria ranged from 2,162,000 to 4,583,800 in 1 ml with a maximum in the layer at a depth of 2 m.

Lake mud at a depth of 7.50 m was richer in bacteria than the lake water itself. In the active part of the mud layer (0–1 cm), the number of bacteria amounted to 3,646,579,000 per ml of crude lake mud, but in the deeper part of the mud (3–5 cm) the number of bacteria increased to 4,087,036,000 per ml of crude mud. Down in the lake mud their number decreased with depth. The minimum number of bacteria was found at a depth of 16–20 cm (1,854,013,000).

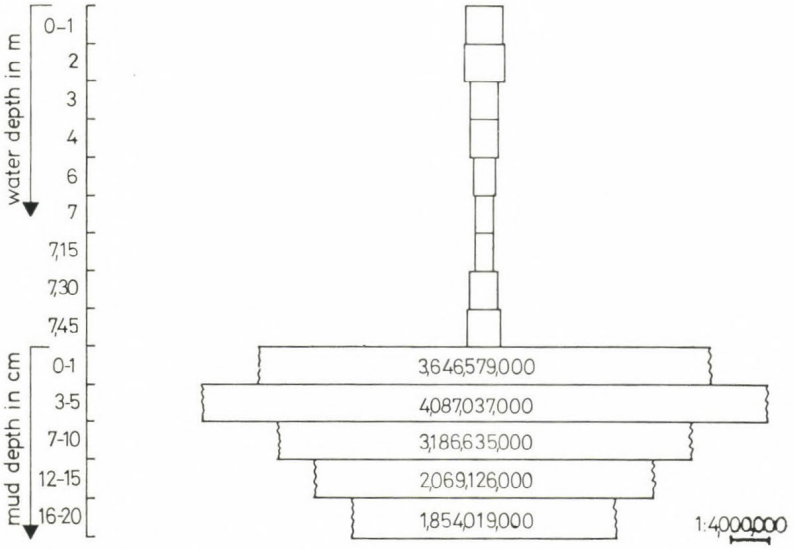


Fig. 2. Vertical distribution of bacterioplankton in the water (number per ml of water), and bacteriobenthos in the mud (number per $cm^3$ of mud) in Lake Castoria (30.9.1961)

According to our microscopical observations the rod forms dominated over cocci, both in the lake water and in the mud (Table 2). The number of rod forms in the water ranged from 91.94 per cent to 97.84 per cent while that of the cocci from 2.16 per cent to 8.06 per cent. The mud of Lake Castoria contained the cocci-form bacteria in a somewhat smaller number (0.12–0.47 per cent) than the lake water, but somewhat more rod forms (99.53–99.88 per cent).

The average biomass of cocci was 0.055 $\mu^3$ and that of rod-shaped bacteria 2.61 $\mu^3$. The total biomass of bacteria in the lake water, from the surface layer to the bottom, varied from 5.43 to 11.34 mg per l. In the mud their total biomass ranged from 4.65 to 10.17 mg per ml of crude mud (Table 3).

Heterotrophic bacteria in Lake Castoria were not found in large amount. In the layers of the lake water, from surface to a depth of 5 m, their number varied from 1,250 to 2,800 per ml of water (Fig. 3). In the contact zone of water with mud their number still increased (from 19,300 to 21,500 bacteria per ml of water).

The lake mud contained plenty of heterotrophic bacteria, with a maximum in the layer of mud from the depths of 3–5 cm (5,057,500 bacteria per ml of crude mud). This maximum was probably caused by the development of

TABLE 2

*Relative percentage of main morphological groups of bacteria in Lake Castoria (30.9.1961)*

| | Morphological group | |
|---|---|---|
| | cocci | rods |
| Water depth, m | | |
| 0–1 | 3.04 | 96.96 |
| 2 | 2.16 | 97.84 |
| 3 | 5.30 | 94.70 |
| 4 | 6.61 | 93.39 |
| 6 | 8.06 | 91.94 |
| 7 | 2.81 | 97.19 |
| 7.15 | 3.70 | 96.30 |
| 7.30 | 5.33 | 94.67 |
| 7.45–7.48 | 7.03 | 92.97 |
| Mud depth, cm | | |
| 0– 1 | 0.33 | 99.67 |
| 3– 5 | 0.47 | 99.53 |
| 7–10 | 0.37 | 99.63 |
| 12–15 | 0.39 | 99.61 |
| 16–20 | 0.12 | 99.88 |

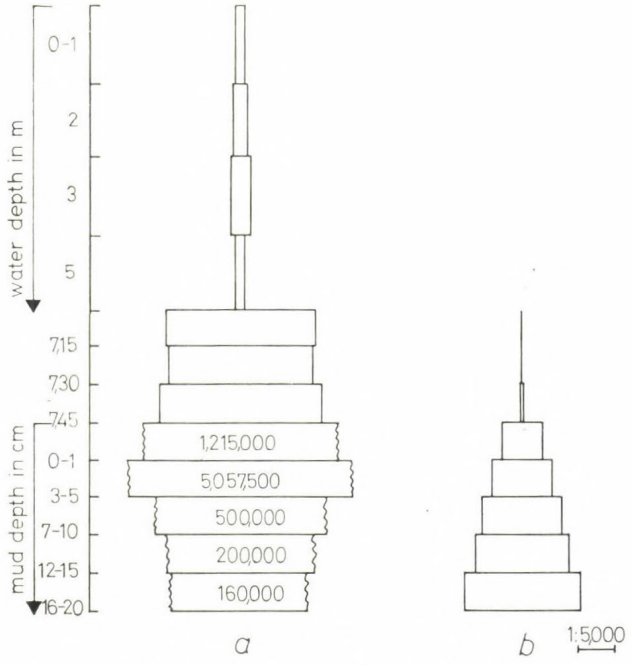


Fig. 3. Vertical distribution of heterotrophic (aerobic) (*a*) and anaerobic bacteria (*b*) per ml in Lake Castoria (30.9.1961)

TABLE 3

*Biomass of bacterioplankton in the lake water and bacteriobenthos in the crude mud of Lake Castoria (30.9.1961)*

| | Biomass of bacteriobenthos, mg per 1 of water | | |
|---|---|---|---|
| | cocci | rods | total |
| Water depth, m | | | |
| 0–1 | 0.007 | 9.67 | 9.677 |
| 2 | 0.012 | 11.38 | 11.392 |
| 3 | 0.008 | 6.85 | 6.858 |
| 4 | 0.011 | 7.12 | 7.132 |
| 6 | 0.011 | 6.15 | 6.161 |
| 7 | 0.003 | 5.49 | 5.493 |
| 7.15 | 0.004 | 5.43 | 5.434 |
| 7.30 | 0.009 | 7.64 | 7.649 |
| 7.50 | 0.017 | 8.08 | 8.098 |
| | Biomass of bacteriobenthos, mg per ml of mud | | |
| | cocci | rods | total |
| Mud depth, cm | | | |
| 0– 1 | 0.006 | 9.196 | 9.202 |
| 3– 5 | 0.010 | 10.159 | 10.169 |
| 7–10 | 0.002 | 8.207 | 8.209 |
| 12–15 | 0.004 | 5.186 | 5.190 |
| 16–20 | 0.003 | 4.651 | 4.654 |

facultative-anaerobic bacteria. In deeper layers this amount decreased ten times (500,000 bacteria per ml crude mud). Down to the 20 cm layers its number decreased 32 times (160,000 bacteria per ml of crude mud).

Anaerobic bacteria in the lake water of Lake Castoria were very small. However, from the surface of the lake water to a depth of 5 m they were not found to be present. In the contact zone of water with mud, their number varied from 170 to 467 bacteria per ml of water. The lake mud contained far more anaerobic bacteria. Downwards in the strata their number increased (from 5,250 to 15,600 anaerobic bacteria per ml of crude mud) (see Fig. 3).

According to Gram's staining method, the Gram-negative bacteria, from the lake water, represented 77.78 per cent, the Gram-positive 20.37 per cent and the Gram-variable 1.85 per cent. The Gram-negative bacteria, from the mud amounted to 28.54 per cent, the Gram-positive to 67.50 per cent, and the Gram-variable to 3.96 per cent.

### *Actinomycetes, yeast-like cells and fungi*

In Lake Castoria there was an abundance of actinomycetes and yeast-like cells. Fungi were found only in the lake water from the surface to a depth of 4 m.

In the lake water the number of actinomycetes ranged from 7,170 to 16,380 per ml of water. Down in the lake mud, in the active parts (0–10 cm),

the actinomycetes attained a maximum, i.e. 4,007,000 per ml of crude mud. In the deeper layers their quantity decreased by half (Fig. 4).

Yeast-like cells were found in all layers of the lake water as well as in the mud. Their quantity varied from 5,100 (surface) to 26,500 per 1 ml of water in a 6-m deep layer. In the mud up to 307,300 cells per 1 ml of crude mud were found (at a depth of 0 to 5 m).

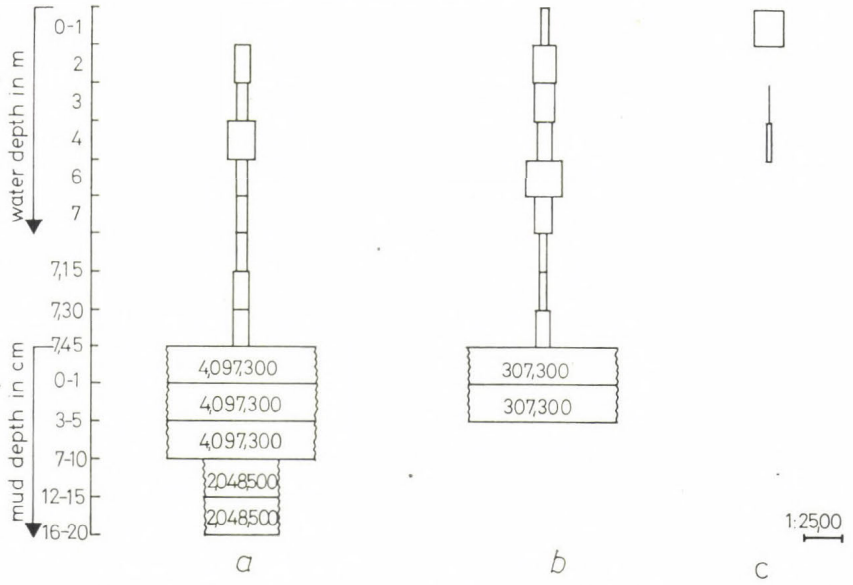


Fig. 4. Vertical distribution of actinomycetes (*a*), yeast-like cells (*b*), and fungi (*c*) per ml of water, and cm³ of mud in Lake Castoria (30.9.1961)

Fungi appeared very rarely in this lake. Their maximum was recorded in the surface water (1,940 per 1 ml of water), in a 4-m deep layer their number decreased 10 times. Down to a depth 7.5 m as well as in the mud they were absent.

## *Phytoplankton*

With the qualitative observation of phytoplankton in Lake Castoria the following species were identified:

### Cyanophyta

*Microcystis aeruginosa* Kg.
*Microcystis flos-aquae* (Wittr.) Kirchn.
*Chroococcus limneticus* var. *distans* Smidt.
*Coelosphaerium kuetzingianum* Naeg.
*Anabaena spiroides* Kleb.
*Anabaena* sp.

*Phormidium mucicola* Naum. et Pestall
*Oscillatoria limnetica* Lemm.
*Lyngbya contorta* Lemm.
*Lyngbya limnetica* Lemm.

Chrysophyta

a. Chrysophyceae

*Dinobryon divergens* Imhof
*Dinobryon* sp.

b. Diatomeae

*Melosira granulata* (E) Ralfs
*Melosira granulata* var. *angustissima* Müller
*Melosira* sp.
*Cyclotella* sp.
*Cyclotella ocellata* Pant.
*Synedra ulna* (Nitsch.) Ehrenb.
*Synedra* sp.
*Cocconeis disculus* (Schum). Cl.
*Nitzschia* sp.
*Gyrosigma attenuatum* (Kütz.) Rabenh.
*Gomphonema constrictum* Ehr.
*Tabellaria* sp.
*Surirella* sp.

Euglenophyta

*Phacus pleuronectes* (O. F. Müller) Duj.
*Phacus* sp.
*Euglena* sp. (two species)

Pyrrophyta

*Ceratium hirundinella* (O. F. Müller) Schrank
*Peridinium* sp.
*Gymnodinium* sp.

Chlorophyta

1. Chlorophyceae

a. Volvocales

*Pandorina morum* Bory
*Eudorina elegans* Ehrenberg

b. Protococcales

*Pediastrum boryanum* (Turp.) Menegh.
*Pediastrum boryanum* var. *granulatum* (Kützing) Al. Braun
*Pediastrum clathratum* (Schroeter) Lemmermann
*Pediastrum duplex* Meyen
*Pediastrum simplex* (Meyen) Lemmermann

*Pediastrum simplex* var. *radians* Lemmermann
*Pediastrum tetras* (Ehrens.) Ralfs
*Tetraedron limneticum* Borge
*Scenedesmus quadricauda* (Turp.) Breb.
*Scenedesmus obliquus* (Turp.) Kütz.
*Scenedesmus* sp.
*Coelastrum microporum* Naegeli
*Coelastrum astroideum* De Notaris

2. Conjugatae

*Closterium* sp.
*Cosmarium* sp. (three species)
*Staurastrum* sp.

The list of algae is not complete because there is no possibility to follow up the seasonal changes and the successive sequences of individual species of plankton. Our investigations and analyses of the results obtained have shown that in the autumn of 1961 the groups of Chrysophyta, Chlorophyceae and Cyanophyta dominated in the species in Lake Castoria. The taxonomic groups of Euglenophyta including four species (of which one *Phacus* and two *Euglena* being present in a small number were not identified), as well as Pyrrophyta and especially the species belonging to Desmidiacea. The species of genera *Closterium*, *Cosmarium* and *Staurastrum* of desmids were not identified. It is well known that the seasonal changes of green algae and Desmidiaceae, as well as three representatives of the above-mentioned group of Pyrrophyta, occur in the summer months. The species of Desmidiaceae appear in relatively greater amounts from the beginning of summer to the beginning of autumn in other Macedonian lakes of Yugoslavia (Kozarov 1957, 1958, 1959). The species from the group of Cyanophyta usually developing more intensively in autumn are not characterized by a more intensive development. The number of the different species of this group is probably greater than it was during our visit to Lake Castoria, because with some exceptions, the species of Cyanophyta may be regarded as the true autonomic plankton (Pearsall 1930, 1932).

Eutrophic waters like Lake Castoria are very rich in phytoplankton. In such waters, as a rule, water bloom appears. But, in October 1961, it did not appear, and the phytoplankton was characterized by a dominance of the taxonomic groups of algae Chrysomonadinae (one unidentified species !) as opposed to the blue-green and other groups of algae. The quantitative value of all other taxonomic groups of algae falls behind the amounts of Chrysomonadinae being very important especially in contributing to the amount of the total mass of phytoplankton. The percentage of the different groups of the phytoplankton during our investigations was as follows: Cyanophyta 1.21 per cent, Chrysomonadinae 79.13 per cent, Diatomeae 14.00 per cent, Pyrrophyta 4.13 per cent, Euglenophyta 0.45 per cent, Protococcales 0.66 per cent, Desmidiaceae 0.50 per cent.

Considering the distribution of algal species it is possible to record certain differences in the distribution of the population density of the individual

planktonic algae. Between the blue-green algae, *Lyngbya limnetica*, *Lyngbya contorta*, *Oscillatoria limnetica* and *Anabaena* show more dense populations, but their vertical distribution is characterized by a larger population of a great number of individuals in the upper layers of the lake water. Similar vertical distribution was observed in the case of Chrysomonadinae and Pyrrophyta and Euglenophyta algal species. However, a complete absence of the individuals of the above-mentioned algal species was recorded from a depth of 5 to 7 metres which was probably due to the development of other taxonomic groups of phytoplankton and to some ecologic factors in the lake water.

Several representatives of planktonic algae of Ditomeae (*Melosira* sp., *Synedra*, *Gyrosigma*) and Protococcales showed relatively higher population density in the water layers being nearer to the lake bottom. Certain Protococcales species of algae (*Pediastrum duplex*, *Scenedesmus quadricauda*, *Tetraedron limneticum*) were also observed sporadically in the upper water layers from a depth of 0 to 4 metres. In contrast the representatives of the planktonic algae of Desmidiaceae appeared from the surface to the bottom of the lake. A similar vertical distribution of the planktonic algae was observed in autumn in Lake Dojran, Yugoslavia (Kozarov 1958).

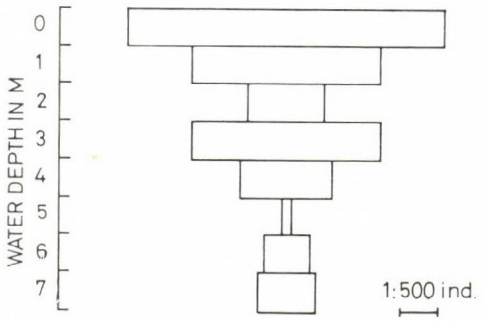


Fig. 5. Vertical distribution of phytoplankton in the water of Lake Castoria (number per ml of water; 30.9.1961)

The vertical distribution of the total phytoplankton is characterized by an abundance in the surface water decreasing with depth. So in the surface water the number of phytoplankton individuals was 4,222 per ml of water (Fig. 5). In the deeper part of the lake water the number of phytoplankton individuals was as follows: at a depth of 1 metre 2,537, at 2 metres 1,049 and in the layers between 4 and 3 metres it varied from 1,302 to 2,027 ind. per ml of water. Down to 7 metres the number of phytoplankton individuals decreased to 800 ind. per ml of water. It is very interesting that the least quantity of individuals was found at the depth of 5 metres (141 ind. per $cm^3$ of water). All this shows that the phytoplankton in the lake water is stratified, the number of phytoplankton individuals decreasing with depth.

The maximum density in October 1961 was characterized by an average quantity of 1,557 ind. per $cm^3$ of water which also points to the production of the eutrophic type.

### *Zooplankton*

The zooplankton of Lake Castoria was very abundant in the period of our investigations (September 1961). The list below shows that Rotatoria, which are represented with 18 species and 1 variety belonging to 13 genera, dominate qualitatively. More of them are cosmopolites and are characteristic of

eutrophic waters. After that come Cladocera represented by two species and finally Copepoda, Mollusca and Insecta, each being represented by only one species.

The list of the zooplankton of Lake Castoria is as follows:

Rotatoria

*Asplanchna priodonta* Gosse
*Ascomorpha ecaudis* Perty
*Triarthra longiseta* Ehrbg.
*Polyarthra trigla* Ehrbg.
*P. euryptera* Wierzejski
*Diurella stylata* Eyferth.
*Trichocerca capucina* (Wierz. and Lach.)
*Tr. pusilla* (Jennings)
*Tr. birostris* (Minkiwicz)
*Pompholyx complanata* Gosse
*Keratella cochlearis* (Gosse)
*K. quadrata* var. *curvicornis* Ehrbg.
*Anuraeopsis fissa* (Gosse)
*Notholca longispina* (Kell.)
*N. striata* (Ehrbg.)
*Ploesoma truncatum* (Lev.)
*Conochiloides dossuarius* (Hudson)
*Pedalion mirum* (Huds.)

Cladocera

*Diaphanosoma brachyurum* (Lievin)
*Daphnia longispina* O. F. Müller

Copepoda

*Thermocyclops hyalinus* (Rehberg)

Insecta

*Chaoborus crystallinus* De Geer

Mollusca

*Dreissena polymorpha* Pallas

We believe that the mesh allowed to pass some tiny Rotatoria and Protozoa, which would certainly enrich the zooplankton composition.

Analysing and comparing this list with the zooplankton list of the other lakes belonging to the Aegean lake zone (Serafimova-Hadžišče 1973) we have arrived at the conclusion that more of the representatives of Rotatoria (*Asplanchna priodonta, Trichocerca capucina, Trichocerca birostris, Pompholix complanata, Notholca longispina*) can be found only in the neigh-

bouring lakes Ostrov and Petersko, but not in this situated at the eastern part of Vardar. The same is the case with *Thermocyclops hyalinus* and *Dreissena polymorpha*.

Even in a quantitative respect (expressed in number of ind. per l of water) Rotatoria is the dominant component. Among them the following are particularly frequent: *Polyarthra euriptera*, *Polyarthra trigla*, *Keratella cochlearis* and *Anuraeopsis fissa*. These four species are dominant planktonic elements during September. The following figures characterize them: *Polyarthra euryptera* 64 ind. per l of water; *Polyarthra trigla* 263 ind. per l; *Keratella cochlearis* 52 ind. per l and *Anuraeopsis fissa* 294 ind. per l. After them come *Ascomorpha ecaudis*, *Asplanchna priodonta*, *Keratella quadrata* and *Pedalion mirum* ranging from 0.8 to 15 ind. per l of water, while the other representatives of Rotatoria are represented by individual specimens of the samples.

*Polyarthra euryptera*, *Polyarthra trigla* and *Anuraeopsis fissa* are in a stage of intensive multiplication. About 40 per cent of the populations of these species lay eggs.

From Cladocera the predominant is *Daphnia longispina*, on the other hand, *Diaphanosoma brachyurum* is represented only in the individual specimens. Only a small number of *Daphnia* laid eggs in laying hole.

The only representative of Copepoda, *Thermocyclops hyalinus*, appears in all nauplius and copepodid stages and male and female adults, too. The total number of nauplius, copepodids and adults is 83 ind. per l of water. Among them nauplii stages I, II, III dominate as well as copepodid stage III. Among the adults females predominate more of which lay eggs. The average number of eggs per female is 20.

*Dreissena polymorpha* in this period is represented only by individual specimens. However, according to research made by Stanković (1951), *Dreissena* is a dominant form among molluscs in the fauna at the bottom, and the shells of *Dreissena* form a clear shell zone, thus being a significant component of the plankton at the period of reproduction.

Although we encountered only single specimens of *Chaoborus crystallinus*, in the plankton, the presence of this species is important because, according to investigations made by Stanković, this species plays a very important role in the fauna at the bottom of the lake.

It is difficult, almost impossible, to draw definite conclusions and make a comparison on the basis of the quantitative data from one collection. However it would be interesting to compare our numerical data with similar ones of the other lakes belonging to the Aegean lake zone.

The plankton production of Lake Dojran was studied by Popovska-Stanković in 1954. According to her data, Cladocera and Copepoda are the dominant components of zooplankton throughout the year, on the other hand, Rotatoria, with the exception of August, when being not found in the plankton, represent small quantities expressed in percentage. They reach their maximum in January participating with 13.34 per cent of the total zooplankton.

In Lake Castoria, on the other hand, at the time of our investigations, Rotatoria were dominant being represented by 86.74 per cent, followed by Copepoda with 13.20 per cent, Cladocera with 0.04 per cent, Insecta with 0.01 per cent and Mollusca with 0.01 per cent.

Our numerical data compared with those of Popovska-Stanković are several times greater.

Figure 6 shows that basically the most important amount of plankton is found in the upper two metres of the water.

The correlation between bacterioplankton, phytoplankton and zooplankton in the water of Lake Castoria is highly evident (Fig. 7). There was a maximal quantity of phytoplankton as well as zooplankton in the layers

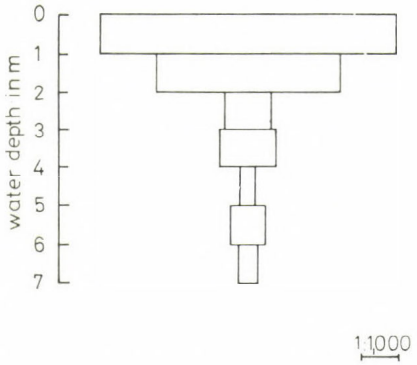


Fig. 6. Vertical distribution of zooplankton in the water of Lake Castoria (number per l of water; 30.9.1961)

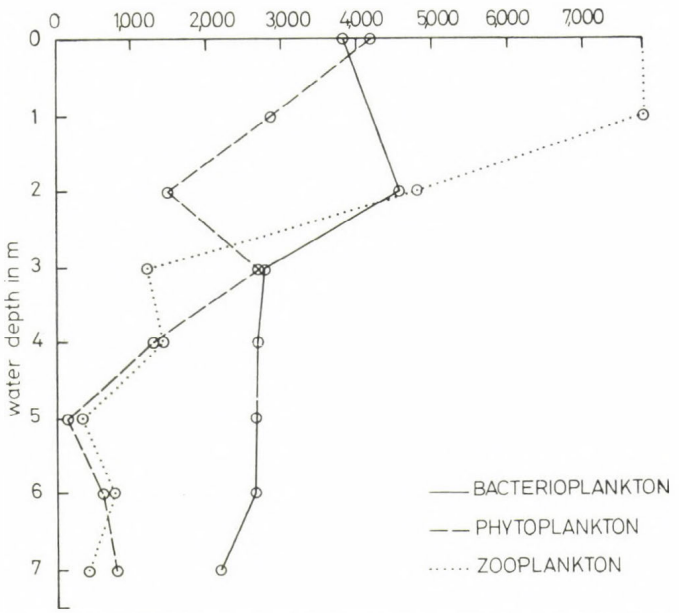


Fig. 7. The correlation of bacterioplankton, phytoplankton and zooplankton in Lake Castoria (30.9.1961). Bacterioplankton is given in terms of number $\times 10^3$ per ml phytoplankton as number per ml and zooplankton as number per l of water

from the surface up to 1 m, but bacterioplankton decreased at that depth. The maximum of the bacterioplankton was found at a depth of 2 m where phytoplankton and zooplankton were decreasing in number. In the layers from 3 m to 7 m, all populations were minimal.

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*Symp. Biol. Hung.*, *15*, pp. 247–254 (1975)

# MACROFAUNAL BIOMASS IN THE SUBMERGED VEGETATION STANDS OF LAKE VELENCE

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## INTRODUCTION

Lake Velence is one of the most interesting European representatives of large, shallow lakes. It is the third largest lake in Hungary, lying 106 m above sea level, extending some 10.5 km NE to SW, with an average width of 2.5 km; its average depth is between 1 and 2 m. The surface area is 26 km$^2$, of which 64 per cent is reedy, while a further 29 per cent of the open water is covered with hair-weeds (Kiss 1972).

Only a few small streams and brooks empty into the lake. The pollution of Lake Velence today is yet but slight, though the natural state of the lake has often been disturbed (dredging, mechanical weeding, water-level regulation).

Since Rezső Maucha's fundamental paper published in 1931, European limnology has shown growing interest in Lake Velence. Many papers discussing the lake have so far raised certain problems regarding hydro- (Donászy 1953) and sediment chemistry (Csajághy 1953), bacteriology (Óláh and Vásárhelyi 1970, Vásárhelyi and Felföldy 1970), public hygiene (Schiefner and Gregács 1964), botany (Borhidi and Balogh 1969, Kiss 1972) and zoology (Berczik 1961, P.-Zánkai 1959), some other papers even ventured as far as to offer solutions. In spite of the great number of data accumulated so far on these topics, the professional opinion of international hydrobiologists is that Hungarian hydrobiology ought to pay a great deal more attention to Lake Velence.

Recently, complex hydrobiological researches on the whole lake have been carried out by a team of workers of the Research Institute for Water Resources Development (VITUKI) headed by Lajos Felföldy. One of the most important accomplishments of these researches was the mapping of the macrovegetation of the lake (Kiss 1972) which revealed extensive stretches of *Vaucheria dichotoma*.

The submerged vegetation playing a significant part in the life of the lake has undergone thorough hydroecological and zoological examination in the past years conducted by the Department of Systematic Zoology and Ecology of the Eötvös Loránd University, Budapest, headed by Árpád Berczik. Here the results of the zoocenological study of some characteristic reed-grass stands are discussed with the principal aim of discovering the differences in the macrofaunal biomass of the water plant population situated next to each other.

## PLACE, TIME AND METHOD OF EXAMINATION

The zoocenological observations were carried out in a hydrochemically characteristic area of Lake Velence, close to the Bird Observatory near Agárd, at 16 collecting sites (Fig. 1).

The research area is situated in the south-western third of the lake. This particular area belongs to the moderately saline parts of the lake. Examinations heretofore have shown a gradual alkalization in a SW–NE direction ascribed to climatic causes (Borhidi and Balogh 1969).

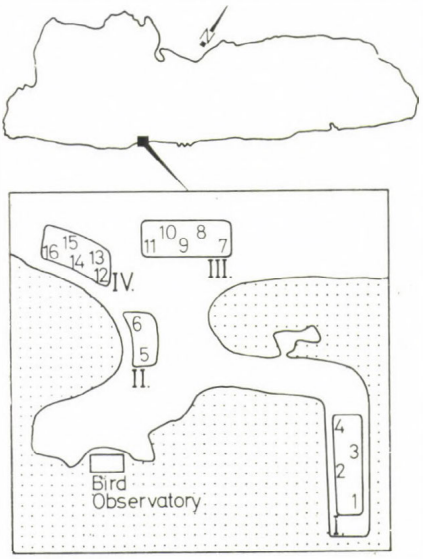


Fig. 1. The lay-out of the collecting sites in the lake

In the various shallow waters the quasi-quantitative examinations indicate a spring and late summer as well as an autumn maximum in the individual numbers of most macrofaunal groups (Berczik 1970).

Considering these results the collecting time was chosen between the 20th and 22nd of August in 1972 hoping that it would coincide with the period of the second population-dynamic maximum. It was assumed, therefore, that the data received on the biomass would show the maximal or near maximal macrofaunal zoomass living in different vegetation stands.

Two different kinds of collecting methods were applied. On various sampling sites composed of *Myriophyllum spicatum*, *Utricularia vulgaris*, *Potamogeton pectinatus*, *Najas marina*, a prism with $50 \times 50$ cm basic area and 120 cm height covered by close-meshed net was used. The appliance was lowered on the vegetation stand at a spot of characteristic density. Then, the entire mass of vegetation was carefully removed from the sediment by divers. Subsequently, the lower opening of the prism was closed and the biomass of the macrofauna was determined. For this purpose the plants were washed and the entire water volume was filtered, using a net of 0.5 mm mesh (Fig. 2).

In the case of *Vaucheria dichotoma* covering large stretches of Lake Velence, a $15 \times 15$ cm, sharp-edged, metal frame covered at the top was used being in turn pressed through the *Vaucheria* stand well into the sediment, then the entire plant material was lifted from the water. In both cases special attention was paid to the careful approach of the collecting sites.

The material was preserved in 4 per cent formalin, sorted out to order and after identification the dry weight of the species was recorded. The specimens were dried at 60 °C. The collected and carefully washed plants were weighed at air-dry state.

Throughout the examinations special attention was devoted to determining the biomass of the faunal fractions of Ephemeroptera, Odonata and Trichoptera which subsequently were compared to the quantitative data

Fig. 2. The first phase of sampling

obtained for other macrofaunal categories. The number of individuals and values of weight were correlated to 1 $m^2$ of surface and 1 kg air-dry vegetation mass, respectively.

## RESULTS AND DISCUSSION

According to the results, four types of collecting sites clearly differing from one another can be distinguished on the basis of dominant plant species, position of the site and the total biomass of the macrovegetation and macrofauna.

I. The first group of collecting sites includes a vegetation stand of about 20 $m^2$ east to the Bird Observatory, composed of *Myriophyllum spicatum* and a lesser cover of *Potamogeton pectinatus* (depth: 70 cm; Fig. 1). The environments of the artificial inlet serving bathing purposes have entirely been cleared of reeds. The total average biomass of the macrovegetation in air-dry state was 162 g per $m^2$. The total average biomass of the macrofauna was 0.109,0 g per $m^2$. Detailed zoocenological data are given in Table 1.

II. The second group includes the *Myrophyllum spicatum* stand of about 10 $m^2$ surface area, lying N to the Bird Observatory (depth: 1 m; Fig. 1). The total average biomass of the macrovegetation was 325 g per $m^2$. The total average biomass of the macrofauna was 1.195,6 g per $m^2$. Detailed zoocenological data are given in Table 2.

III. The third group comprises the *Vaucheria dichotoma* stand situated N to the Bird Observatory (depth: 125 cm). The total average biomass of the

TABLE 1

*Average biomass of macroorganisms at station group No. I*

| Taxa | A | B | C | D |
|---|---|---|---|---|
| Ephemeroptera | | | | |
| *Cloeon dipterum* (L.) | 28 | 0.003,2 | 170.8 | 0.019,5 |
| *Caenis horaria* (L.) | 20 | 0.002,4 | 122.0 | 0.014,6 |
| Odonata | | | | |
| *Ischnura pumilio* (Charp.) | 8 | 0.021,6 | 48.8 | 0.131,7 |
| *Agrionidae* (juv.) | 64 | 0.006,4 | 390.4 | 0.039,0 |
| *Sympetrum* sp. (juv.) | — | — | — | — |
| Trichoptera | | | | |
| *Echnomus tenellus* (Klap.) | — | — | — | — |
| *Cyrnus* (*flavidus* MacLach?) | 8 | 0.001,6 | 48.8 | 0.009,7 |
| Hirudinoidea | — | — | — | — |
| Mollusca | 4 | 0.001,2 | 24.4 | 0.007,3 |
| Isopoda | — | — | — | — |
| Coleoptera | 4 | 0.002,4 | 24.4 | 0.014,6 |
| Heteroptera | 8 | 0.001,6 | 48.8 | 0.001,6 |
| Lepidoptera | 8 | 0.004,6 | 48.8 | 0.028,1 |
| Diptera | | | | |
| Chaoboridae | — | — | — | — |
| Chironomidae (larvae) | 728 | 0.059,2 | 4,440.8 | 0.361,1 |
| Chironomidae (pupae) | 44 | 0.004,8 | 268.4 | 0.029,2 |
| Hydracarina | — | — | — | — |
| Total | 924 | 0.019,0 | 5,636.4 | 0.656,4 |

A = average No. per $m^2$; B = average dry weight per $m^2$; C = average No. per kg dry plant weight; D = average dry weight per kg dry plant weight.

algal stand was 165.5 g per $m^2$. The total average biomass of the macrofauna was 3.981,5 g per $m^2$. Detailed zoocenological data are given in Table 3.

IV. The fourth group comprises mainly *Utricularia vulgaris* and a smaller cover of *Potamogeton pectinatus* and *Najas marina*; it is situated NW from the Observatory. The total average biomass of the macrovegetation was 158.4 g per $m^2$. The total average biomass of the macrofauna was 1.092,5 g per $m^2$. Detailed zoocenological data are given in Table 4.

It is a clearly seen from the tables that 3.4–15.7 per cent of the macrofauna biomass is made up of Ephemeroptera, while Odonata and Trichoptera are represented by 0.0–25.6 and 0.3–9.1 per cent, respectively.

The biomass formation of the mud inhabiting *Caenis horaria* larvae may be a good indicator as regards sedimentation at the area covered with macrovegetation. The most intensive sedimentation occurs in those vegetation

TABLE 2

*Average biomass of macroorganisms at station group No. II*

| Taxa | A | B | C | D |
|---|---|---|---|---|
| Ephemeroptera | | | | |
| *Cloeon dipterum* (L.) | 228 | 0.171,2 | 864 | 0.513,6 |
| *Caenis horaria* (L.) | 44 | 0.016,8 | 132 | 0.050,4 |
| Odonata | | | | |
| *Ischnura pumilio* (Charp.) | 12 | 0.030,4 | 36 | 0.091,2 |
| *Agrionidae* (juv.) | — | — | — | — |
| *Sympetrum* sp. (juv.) | — | — | — | — |
| Trichoptera | | | | |
| *Echnomus tenellus* (Klap.) | 16 | 0.019,2 | 48 | 0.074,4 |
| *Cyrnus* (*flavidus* MacLach?) | — | 0.024,8 | 12 | 0.057,6 |
| Hirudinoidea | — | — | — | — |
| Mollusca | 32 | 0.001,6 | 96 | 0.004,8 |
| Isopoda | — | — | — | — |
| Coleoptera | — | — | — | — |
| Heteroptera | — | — | — | — |
| Lepidoptera | — | — | — | — |
| Diptera | | | | |
| Chaoboridae | 8 | 0.025,2 | 24 | 0.075,6 |
| Chironomidae (larvae) | 1,692 | 0.892,8 | 5,076 | 2.678,4 |
| Chironomidae (pupae) | 40 | 0.008,8 | 120 | 0.026,4 |
| Hydracarina | 24 | 0.004,8 | 72 | 0.014,4 |
| Total | 2,160 | 1.195,6 | 6,480 | 3.586,8 |

A = average No. per m²; B = average dry weight per m²; C = average No. per kg dry plant weight; D = average dry weight per kg dry plant weight.

stands (e.g. *Vaucheria dichotoma, Utricularia vulgaris*) in which the number of *Caenis horaria* larvae is very high; in other biotopes the process is comparatively slower.

The extensive *Vaucheria dichotoma* stands of Lake Velence proved to be the richest in macrofauna, where, let alone a few taxa or species, the molluscans appeared in a strikingly high percentage. Their quantity outstripped even that of the Chironomidae larvae, whereas the average macrofaunal biomass in the *Myriophyllum spicatum* stand found in the artificial inlet was markedly low.

The detailed taxonomic elaboration of the three macrofaunal orders has shown that within a small area no qualitative difference may be ascertained in the zoocenosis of the hair-weed population of different species. This finding was confirmed by previous detailed taxonomic researches, too (Andrikovics 1973), which had been carried out on other orders of the macrofauna. The tables do not comprise other species of the macrofauna except

TABLE 3

*Average biomass of macroorganisms at station group No. III*

| Taxa | A | B | C | D |
|---|---|---|---|---|
| Ephemeroptera | | | | |
| *Cloeon dipterum* (L.) | — | — | — | — |
| *Caenis horaria* (L.) | 44 | 0.137,6 | 264 | 0.825,6 |
| Odonata | | | | |
| *Ischnura pumilio* (Charp.) | — | — | — | — |
| *Agrionidae* (juv.) | — | — | — | — |
| *Sympetrum* sp. (juv.) | — | — | — | — |
| Trichoptera | | | | |
| *Echnomus tenellus* (Klap.) | 44 | 0.363,1 | 264 | 2.178,6 |
| *Cyrnus* (*flavidus* MacLach. ?) | — | — | — | — |
| Hirudinoidea | — | — | — | — |
| Mollusca | 3,774 | 1.252,0 | 22,644 | 7.512,0 |
| Isopoda | 355 | 0.612,7 | 2,130 | 3.676,2 |
| Coleoptera | — | — | — | — |
| Heteroptera | — | — | — | — |
| Lepidoptera | — | — | — | — |
| Diptera | | | | |
| Chaoboridae | — | — | — | — |
| Chironomidae (larvae) | 1,198 | 1.451,8 | 7,192 | 8.710,8 |
| Chironomidae (pupae) | 44 | 0.164,3 | 264 | 0.985,8 |
| Hydracarina | — | — | — | — |
| Total | 5,459 | 3.981,5 | 32,758 | 23.889,0 |

A = average No. per m²; B = average dry weight per m²; C = average No. per kg dry plant weight; D = average dry weight per kg dry plant weight.

those of the orders Ephemeroptera, Odonata and Trichoptera. The following list shows the most characteristic and commonest species:

Mollusca: *Armiger crista, Planorbis spirorbis*; Hirudinoidea: *Piscicola geometra; Diptera larvae; Chaoborus crystallinus* and the species of the subfamily of Orthocladiinae in Chironomidae; Lepidoptera: *Paraponyx stratiotata, Nymphula nympheata*; Heteroptera: *Micronecta pusilla, Cymatia coleoptrata, Naucoris cimicoides*; Isopoda: *Asellus aquaticus*; Hydracarinae: *Hydrodroma despiciens* and the species of *Arrenurus* and *Piona*. All of them are common eurytrophic species.

As a result of these researches, concrete quantitative data on the zoocenoses of the hair-weed stands in Lake Velence were obtained. A comparison of the macrofaunal biomass of the different plant stands shows that zoocenosis limited primarily by extreme water climatic conditions will respond

TABLE 4

*Average biomass of macroorganisms at station group No. IV*

| Taxa | A | B | C | D |
|---|---|---|---|---|
| Ephemeroptera | | | | |
| *Cloeon dipterum* (L.) | 120 | 0.029,2 | 756 | 0.183,9 |
| *Caenis horaria* (L.) | 36 | 0.076,0 | 226.8 | 0.478,8 |
| Odonata | | | | |
| *Ischnura pumilio* (Charp.) | — | — | — | — |
| *Agrionidae* (juv.) | — | — | — | — |
| *Sympetrum* sp. (juv.) | 4 | 0.011,2 | 25.2 | 0.070,5 |
| Trichoptera | | | | |
| *Echnomus tenellus* (Klap.) | — | — | — | — |
| *Cyrnus* (*flavidus* MacLach.?) | 4 | 0.003,6 | 25.2 | 0.022,6 |
| Hirudinoidea | 4 | 0.002,2 | 25.2 | 0.138,6 |
| Mollusca | 308 | 0.014,0 | 1,940.4 | 0.088,2 |
| Isopoda | 4 | 0.001,8 | 25.2 | 0.011,3 |
| Coleoptera | — | — | — | — |
| Heteroptera | 12 | 0.000,7 | 75.6 | 0.004,4 |
| Lepidoptera | — | — | — | — |
| Diptera | | | | |
| Chaoboridae | 4 | 0.004,8 | 25.2 | 0.030,2 |
| Chironomidae (larvae) | 3,424 | 0.819,6 | 21,571 | 5.163,4 |
| Chironomidae (pupae) | 64 | 0.025,2 | 403.2 | 0.158,7 |
| Hydracarina | 16 | 0.004,2 | 100.8 | 0.026,4 |
| Total | 4,000 | 1.092,5 | 25,299.8 | 6.377,0 |

A = average No. per m²; B = average dry weight per m²; C = average No. per kg dry plant weight; D = average dry weight per kg dry plant weight.

in variously situated stands of different sedimentary processes to diverse population and food supply conditions by changing the quantitative composition of the macrofauna.

*

*Acknowledgements.* The author is greatly indebted to Mr. Jenő Radetzky, warden of the Bird Observatory, and to divers Ottó Bojtár, István Kürti and József Sármány for their keen and precise work.

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*Symp. Biol. Hung.*, *15*, pp. 255–263 (1975)

# SEASONAL AND ANNUAL VARIATION OF THE POPULATION DENSITY AND BIOMASS OF THE BOTTOM-FAUNA IN THE DEEPEST WATERS OF LAKE DOJRAN, MACEDONIA

by

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There are about twenty lakes, situated in the European region of the Aegean Sea zone, with their major part being in the territory of Macedonia. One of them is Lake Dojran, situated on the Yugoslavian–Greek frontier. According to Cvijić (1911) the present Lake Dojran is the remains of Lake Peonic, being three times bigger and ten times deeper than the former one. The surface of Lake Dojran is 42.66 km², with a maximum depth of about ten meters (Fig. 1).

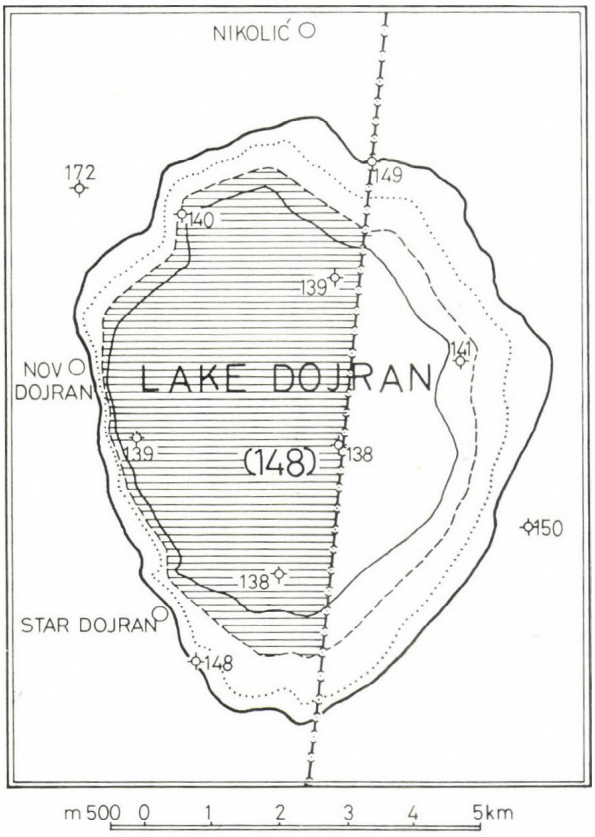


Fig. 1. Survey map of Lake Dojran (cross-hatching denotes the explored area)

TABLE 1

*Average value of the population density (ind. per m²) of different animal groups and species, in the composition of the zoobenthos in the deepest water of Lake Dojran*

| Groups and species | 1962 | 1963 | 1964 | 1965 | 1967 |
|---|---|---|---|---|---|
| Triclada | — | 0.2 | — | — | — |
| Rhabdocoela | 78.8 | 43.7 | 39.4 | 19.9 | 37.0 |
| Nematoda | 371.9 | 279.0 | 189.8 | 95.2 | 329.3 |
| Oligochaeta: | | | | | |
| *Euilyodrilus hammoniensis* | 2,524.4 | 1,947.5 | 1,464.1 | 2,382.5 | 3,573.2 |
| other oligochaetes | 150.4 | 31.5 | 52.0 | 58.6 | 178.6 |
| Hirudinea: | | | | | |
| *Erpobdella octoculata* | 4.6 | 5.2 | 0.7 | 0.4 | 3.7 |
| *Hemiclepsis marginata* | 1.1 | 0.4 | 0.5 | — | — |
| *Glossiphonia complanata* | 0.5 | — | — | — | — |
| Ostracoda | 119.0 | — | 1.7 | 34.2 | 22.2 |
| *Asellus aquaticus* | 4.0 | 12.6 | 0.01 | — | — |
| *Rivulogammarus triacanthus* | 43.7 | 23.5 | 11.4 | 15.1 | — |
| Hydracarina | 0.2 | — | — | — | — |
| Chironomidae: | | | | | |
| *Chironomus plumosus* | 458.2 | 324.3 | 736.9 | 850.7 | 913.1 |
| other chironomides | 1,453.4 | 933.8 | 1,061.9 | 1,128.7 | 1,728.6 |
| *Culicoides* sp. | 29.9 | 35.4 | 27.9 | 14.4 | 14.8 |
| *Chaoborus crystallinus* | 6,447.2 | 9,921.0 | 5,895.1 | 2,041.5 | 6,487.9 |
| *Valvata piscinalis* | 5.9 | 5.9 | 0.01 | 0.7 | — |
| Sphaeriidae | 2.1 | — | — | — | — |
| *Dreissena polymorpha* | 35.5 | 11.1 | 5.3 | 3.5 | — |
| *Anodonta* sp. | — | 0.4 | 0.01 | — | — |
| *Unio pictorum* | 0.5 | 1.0 | 2.0 | 2.0 | 3.7 |

Lake Dojran represents a typical eutrophic lake from the Aegean lake's zone conditioned by edaphic, morphometrical and climatic peculiarities (Stanković 1951). Recently, its eutrophy has been confirmed by studying the metabolism of the lake (Petrović 1969) and the biomass of zooplankton (Popovska-Stanković 1965). This proposition has been supported by the results of the bottom animal investigations of the same Lake (Stanković 1951, Stojkovski 1959 and Šapkarev 1959, 1964, 1968*a*, *b*).

The material was obtained by using a Birdge–Ekman dredge. Quantitative samples were taken from ten stations at the deepest part of the lake at the end of every month from 1962 up to 1967, except in 1966. The total number of the quantitative samples collected in this period was about thousand.

## RESULTS OF INVESTIGATIONS

The analyses of the population density and biomass of some more important species or groups of this animal community throughout the year have reveal-

ed that they display seasonal changes with more or less obvious minimum and maximum.

During the investigation period the most important groups of the bottom animals in the deepest waters of Lake Dojran were oligochaetes [almost only *Euilyodrilus hammoniensis* (Mich.)], and flies presented with two families: Chironomidae, mainly with *Chironomus plumosus* (L.) and Culicidae with the remarkable species *Chaoborus crystallinus* (De Geer).

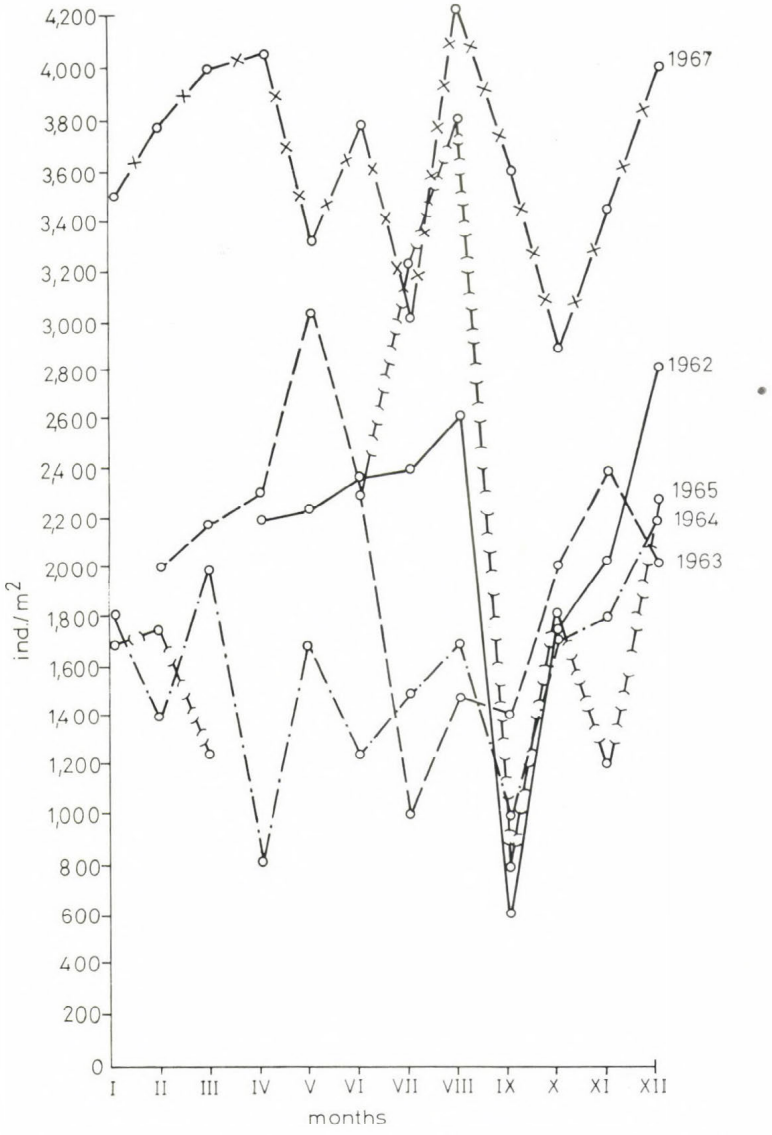


Fig. 2. Seasonal variation of the population density of *Euilyodrilus hammoniensis* Mich. in the deep region of Lake Dojran during 1962–1967

The abundance of the different groups and species, resp., included in this community is illustrated by Table 1. The greatest density of population was shown by Culicidae – *Chaoborus crystallinus*, resp. The average value of the results during the investigation period shows that *Ch. crystallinus* has been colonized in the deepest region of the Lake with 4,452.6 individuals per $m^2$. On the second place comes Oligochaeta in which the total population density (2,473.5 ind. per $m^2$) of the dominating species *Euilyodrilus hammoniensis* amounts to 96.1 per cent (2,378.3 ind. per $m^2$), while that of the other oligochaetes only to 3.9 per cent (94.2 ind. per $m^2$). With a somewhat more reduced population density than that of Oligochaeta this lake region is inhabited by Chironomidae (1,917.9 ind. per $m^2$) of which *Chironomus plumosus* represents 34.2 per cent (656.6 ind. per $m^2$) and other chironomides represent 65.8 per cent (1,261.3 ind. per $m^2$).

All other groups, except Nematoda (253.0 ind. per $m^2$), inhabit the bottom of the deepest lake region with a small population density under 100 ind. per $m^2$ (Rhabdocoela, Hirudinea, Gammaridae, Heleidae, Gastropoda and Bivalvia) or they occur sporadically (like Triclada, Ostracoda, Asellidae, Hydracarina).

## SEASONAL VARIATION OF POPULATION DENSITY AND BIOMASS

The analyses of the population density and biomass of some more important species or groups of this animal community throughout the year have revealed that they display seasonal changes with more or less obvious minimum and maximum (Table 1).

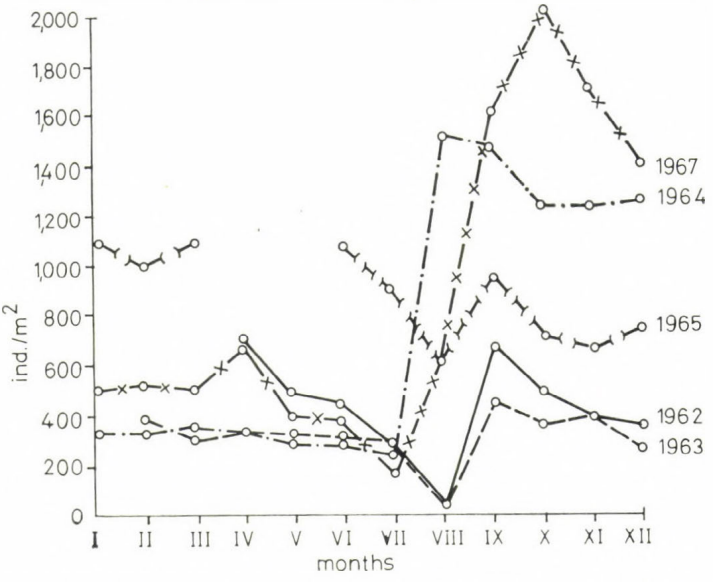


Fig. 3. Seasonal variation of the population density of *Chironomus plumosus* L. in the deep region of Lake Dojran during 1962–1967

During 1962 the dominant species of oligochaetes, *Euilyodrilus hammoniensis* showed two maxima, in August and December, and one minimum of population density in September. The same was established during 1965 and 1967, while in 1963 and 1964 with the difference that the maximum in August and the minimum in September occurred in May and in July, resp. (Fig. 2).

The biomass of *E. hammoniensis* showed a decreased value in the summer months (e.g. in July 1964, 1.742 g per $m^2$) and an increased one in the spring months (e.g. in March 1964, 7.517 g per $m^2$). The variation of the population density of *E. hammoniensis* during the year determines the variation of all Oligochaeta, because all other species of oligochaetes display an insignificant population density.

The dominant species of chironomides, *Ch. plumosus*, during 1962 showed one minimum of population density in August and one maximum in September. The same was stated during 1963 and 1965 but in 1964 and 1967, with the difference that minima and maxima were reached a month earlier (while the maximum of 1967 a month later, see Fig. 3).

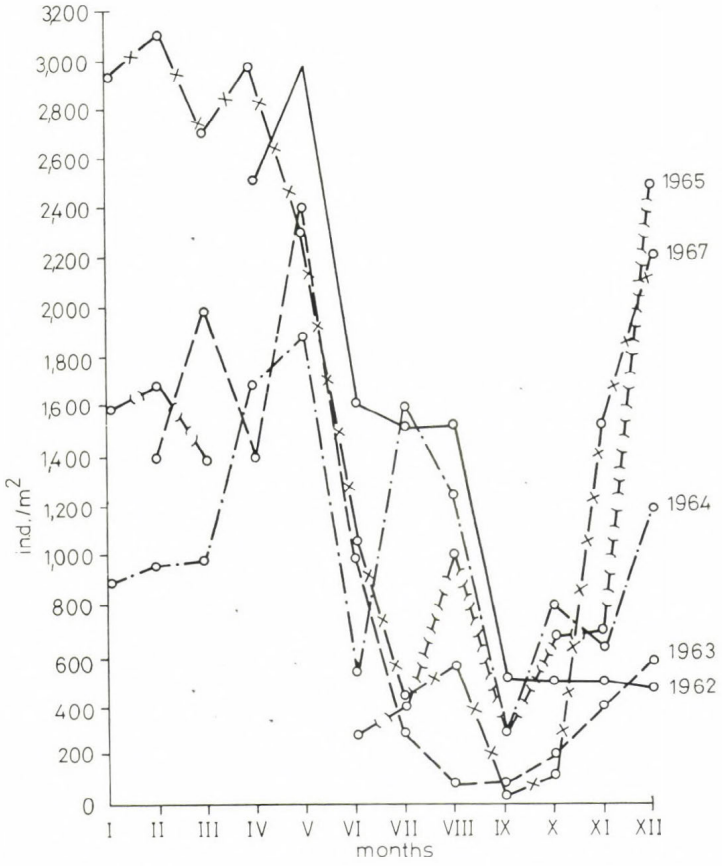


Fig. 4. Seasonal variation of the population density of Chironomidae (without *Chironomus plumosus*) in the deep region of Lake Dojran during 1962–1967

The biomass of *Ch. plumosus* during 1962, 1963 and 1965 reached a maximum in March or April (e.g. in April 1962, 21.287 g per $m^2$) and a minimum in August (e.g. in August 1962, 1.244 g per $m^2$), except for 1964 and 1967 when the minimum of biomass appeared in July and the maximum in September and October, resp. (in the autumn months).

The population density and biomass of all other chironomides show a maximum in the winter months, and at the beginning of spring, with a minimum in the summer months and at the beginning of autumn (Fig. 4).

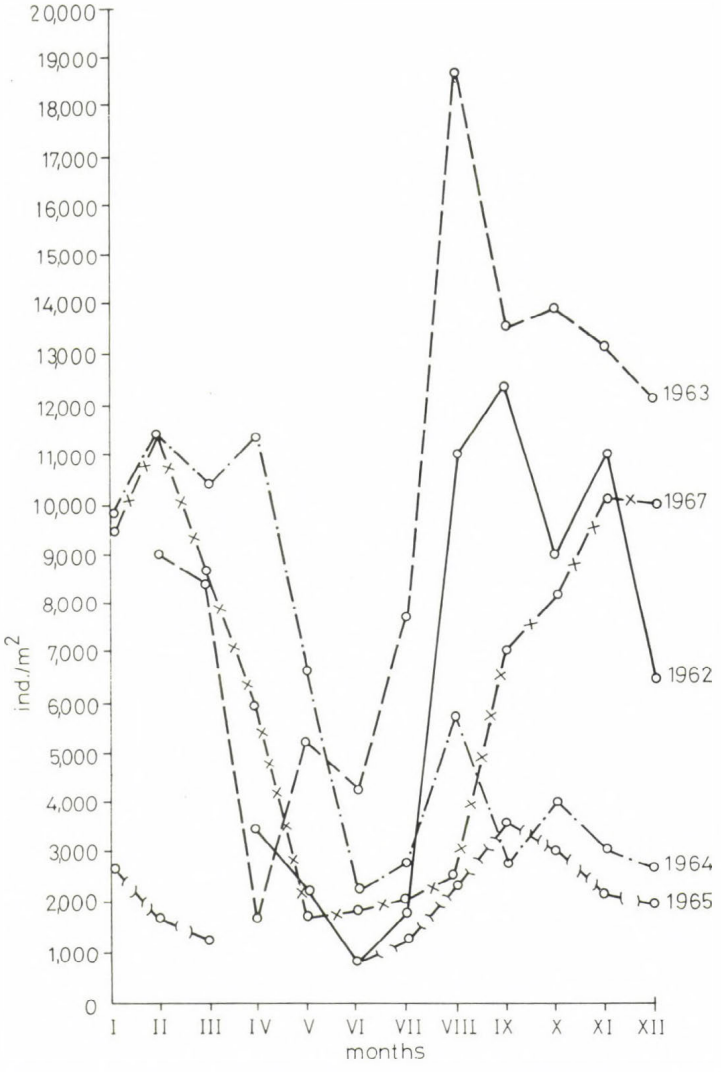


Fig. 5. Seasonal variation of the population density of *Chaoborus crystallinus* (De Geer) in the deep region of Lake Dojran during 1962–1967

One more species of this community of zoobenthos of Lake Dojran, being otherwise characteristic of the variation of the population density in the deepest region, is *Ch. crystallinus* (Culicidae). During the five years the population density showed a minimum and a maximum in August, and September, resp., except for a minimum in April, 1963 (Fig. 5).

In this period a minimum of biomass of *Ch. crystallinus* appeared during summer (e.g. in July 1967, 3.713 g per $m^2$) and a maximum in the winter months (e.g. in February 1967, 28.528 g per $m^2$).

All other species, and groups, resp. of the bottom fauna showed a very slight population density and biomass.

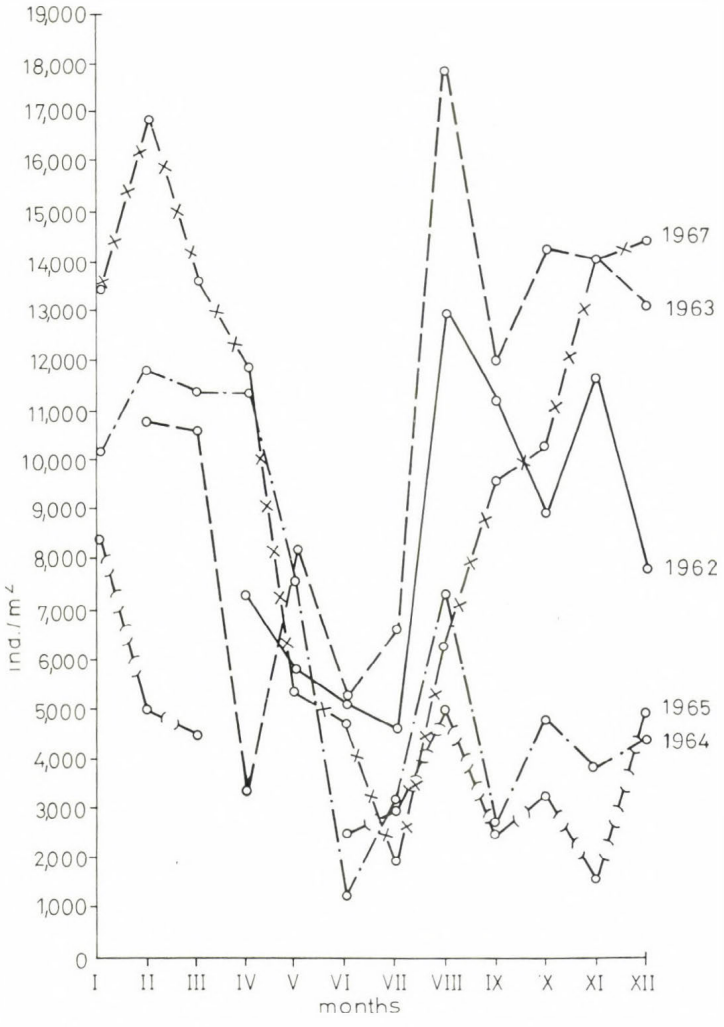


Fig. 6. Seasonal variation of the population density of all zoobenthos in the deep region of Lake Dojran during 1962–1967

The total zoobenthos of the deepest part of the lake showed a minimal population density mostly in June–July and a maximal one in August–September (Fig. 6). The biomass of the total zoobenthos showed the same variation like that of the biomass of *Ch. crystallinus*, e.g. in March 1964, 53.715 g per $m^2$ and in July 12.761 g per $m^2$ wet weight.

## ANNUAL VARIATIONS OF POPULATION DENSITY AND BIOMASS

The average number of individuals per $m^2$ during 1962–1967 for *E. hammoniensis*, *Ch. plumosus* and other chironomides, *Ch. crystallinus* and all zoobenthos for the deep water area of the lake is given in Fig. 7.

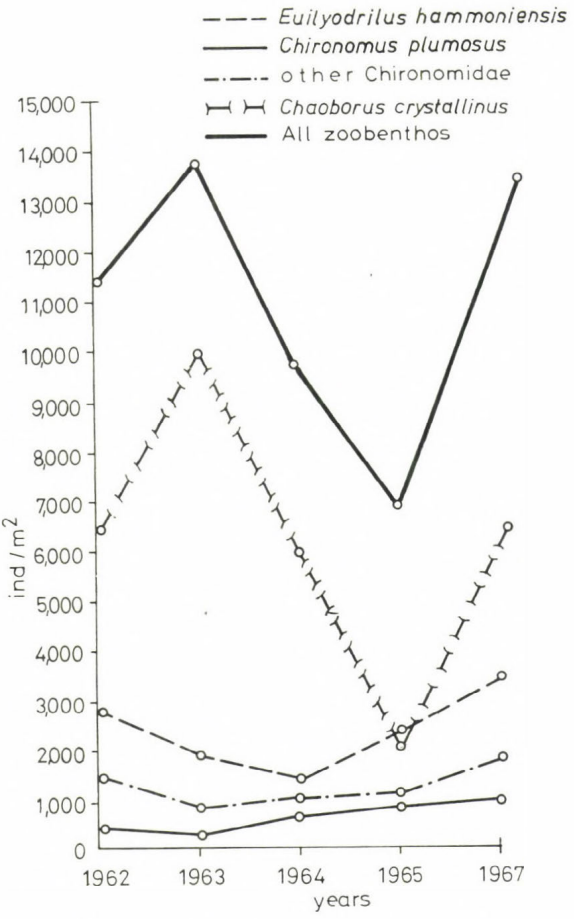


Fig. 7. Annual variation of the density of population of *Chironomus plumosus*, other Chironomidae, *Euilyodrilus hammoniensis*, *Chaoborus crystallinus* and all zoobenthos in the deep region of Lake Dojran during 1962–1967

During 1962–1967, *E. hammoniensis* showed a maximal population density and biomass in 1967 (3,752 individuals, 5.956 g wet weight per $m^2$) and a minimum in 1964 (1,604 individuals, 3.042 g wet weight per $m^2$.

*Ch. plumosus* as a dominant species of the biomass of chironomides showed the smallest population density and biomass in 1963 (324 individuals, 8.749 g wet weight per $m^2$) and the biggest one in 1967 (913 individuals, 22.246 g wet weight per $m^2$) but the other chironomides reached a minimum of population density and biomass in 1963 (934 individuals, 1.168 g wet weight per $m^2$) and a maximum in 1967 (1,728 individuals, 2.190 g wet weight per $m^2$).

The annual variation of population density and biomass of *Chaoborus crystallinus* showed a maximum in 1963 (9,921 individuals, 22.173 g wet weight per $m^2$) and a minimum in 1965 (2,042 individuals, 4.885 g wet weight per $m^2$), similarly to the population density and biomass of *E. hammoniensis*.

Finally, the annual variation of the population density and biomass of the total zoobenthos in the deepest water area of Lake Dojran is determined at first by the variation of the population density and biomass of *Ch. crystallinus*.

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*Symp. Biol. Hung.*, *15*, pp. 265–272 (1975)

# DIE ENTWICKLUNG DER BESIEDLUNG IN EINEM NEUENTSTANDENEN GEWÄSSER, DARGESTELLT AN DEN CILIATEN UND WASSERKÄFERN

von

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## EINLEITUNG

Werden Braunkohlentagebaue stillgelegt, so ist es meist nicht möglich, mit vertretbarem Aufwand diese riesigen verbleibenden Löcher wieder völlig zu füllen. Zwar steht hierfür theoretisch der gesamte Abraum zur Verfügung, ein Defizit ergibt sich aber durch die andernorts verwendete Braunkohle.

Meist sammelt sich bereits nach kurzer Zeit durch Zustrom aus dem Untergrund und durch Niederschläge Wasser in diesen Löchern: es bilden sich die Braunkohlenrestgewässer, verschiedentlich auch Restgewässer oder Tagebaugewässer genannt. In den Braunkohlenrevieren, so etwa dem mitteldeutschen und dem rheinländischen, stellen diese Restgewässer wesentliche Elemente der Landschaft dar. Somit bieten sie Anreiz für Untersuchungen über ihre Bedeutung, Entwicklung und Nutzung. Obwohl bereits eine Reihe diesbezüglicher Untersuchungen vorliegen, sind unsere Kenntnisse über die Entwicklungsrichtung und -geschwindigkeit der Biozönosen derartiger Gewässer noch recht lückenhaft. Erst Herbst (1966) hat diesem Gesichtspunkt stärker Rechnung getragen, indem er verschieden alte Restgewässer untersuchte, was ihn in die Lage versetzte, interpolierend Entwicklungstendenzen anzugeben. Präzisere Unterlagen erbringen jedoch erst längerfristige Untersuchungen ein und desselben Gewässers. Deshalb wurde der Obersee, dessen Auffüllung im Herbst 1964 begann, in den Jahren 1965 bis 1970 monatlich einmal chemisch und biologisch untersucht.

## LAGE UND MORPHOLOGIE DES GEWÄSSERS

Der etwa 6 ha große Obersee liegt westlich Kölns in der Nähe des Ortes Liblar. Er ist meist 1 bis 2 m, maximal bis 3,5 m tief. Die Ufer fallen nicht steil ab, sondern gestatten die Ausbildung eines breiten Röhrichtgürtels, der sich in einzelnen Bereichen auch bereits entwickelt hat. Der Gestaltung der Ufer kommt insofern große Bedeutung zu, zumal bei fischereilich genutzten Gewässern, als sich im Litoral ein wesentlicher Teil der Fischnährtiere entwickelt. Remane und Herre (1937) haben deshalb diesen Gesichtspunkt nach ihren Untersuchungen an steilufrigen, folglich nährtierarmen und fischereilich wenig ertragreichen Restgewässern sehr stark in den Vordergrund gestellt.

Die Flachheit, die eine Durchlichtung des gesamten Wasserkörpers und somit das Aufkommen unterseeischer Wiesen gestattet, weist den Obersee nach limnologischer Terminologie als Weiher aus.

Wie nach den zahlreich mitgeteilten Analysendaten über den Chemismus von Restgewässern (Hilse 1958, Kalbe 1958/59, Müller 1959, 1961, Bauer 1963, Pietsch 1965, Herbst 1966, Campbell und Lind 1969, Trahms 1972) zu erwarten ist, zeichnet sich auch der Obersee durch einen extrem hohen Sulfatgehalt aus. Die dominierende Kalzium/Sulfat-Komponente

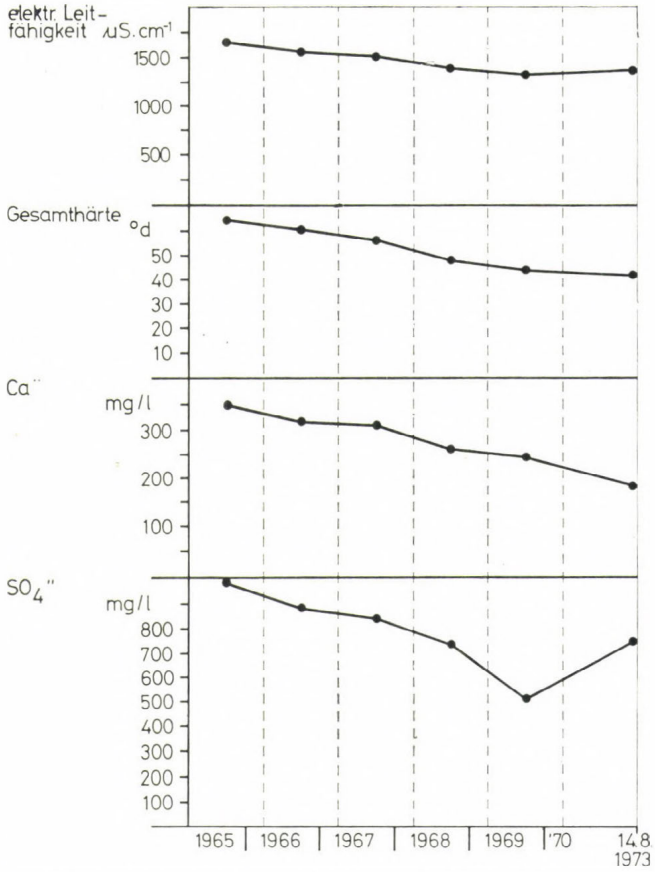


Abb. 1. Der Verlauf einiger chemischer Kenngrößen im Braunkohlenrestgewässer Obersee. Dargestellt sind die Mittelwerte von 5 Jahresreihen (die sich jeweils vom März bis zum Februar erstrecken) und einzelne Meßwerte vom 14.8.1973

bedingt auch eine erhebliche Wasserhärte, zu der in der Anfangsphase die Karbonate nur unwesentlich beitragen. (Das Verhältnis Karbonathärte zu Gesamthärte beträgt etwa 1 : 10.) Die Reaktion des Wassers lag meist bei pH = 8. Ein weiteres Charakteristikum der Restgewässer ist deren Nährstoffarmut. Im Obersee betrugen die Konzentrationen im Schnitt für $PO_4$—P 0,08 mg/l, für $NH_4$—N 0,22 mg/l und für $NO_3$—N 0,18 mg/l. Wie Herbst (1966) nachwies, klingen mit zunehmendem Alter der Restgewässer die extremen chemischen Verhältnisse etwas ab. Abbildung 1 verdeutlicht,

daß dieser Normalisierungsprozeß relativ zügig voranschreitet. Für die hier nicht mit dargestellten Nährstoffe P und N zeichnet sich dagegen während der 6jährigen Untersuchungsdauer noch keine Erhöhung ab.

## BIOZÖNOTISCHE ASPEKTE

### *Die Ciliatenzönose*

Die Aussagen über die Entwicklung des Ciliatenbestandes gründen sich vor allem auf Aufwuchsproben. Dazu wurden an verschiedenartigen Stellen des Litorals Objektträger exponiert, um bei der Beurteilung der Bestandsent-

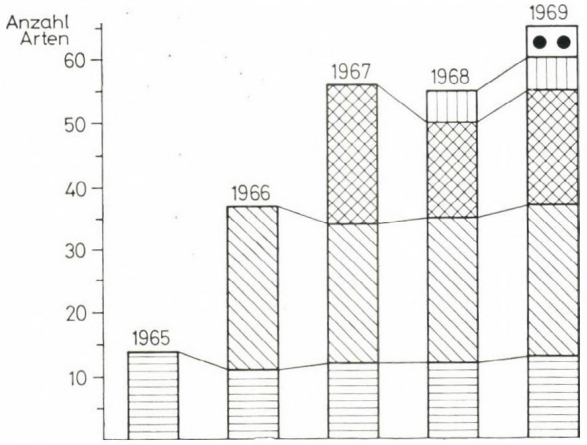


Abb. 2. Fluktuationsanalyse der Ciliatenzönose im Obersee für die Jahre 1965 bis 1969. Durch die unterschiedlichen Schraffuren wird der Anteil der neu hinzukommenden Arten und der der bereits in früheren Jahren beobachteten Arten gekennzeichnet

wicklung Besonderheiten des Mikrobiotops einzuschränken. Alle an einem Probennahmetag an den verschiedenen Stationen gefundenen und sicher determinierten Ciliaten sowie 2 Suktorienarten (*Metacineta mystacina* ab November 1967 und *Heliophrya riederi* ab November 1968) werden in die Betrachtungen einbezogen.

In Abbildung 2 ist die Entwicklung der Ciliatenzönose dargestellt. Zu dem relativ bescheidenen Bestand von 14 Arten im Jahre 1965* gesellen sich im folgenden Untersuchungsjahr (1966) weitere 23 Arten. Bereits nach dem 3. Jahr ist die Ciliatengemeinschaft weitgehend konsolidiert, der Artenzuwachs in den beiden anschließenden Jahren ist geringfügig (1968 und 1969 jeweils nur 5 Arten). Daß die Artendichte der Ciliaten im Obersee nach

* Da einige Arten während der Initialphase nur in Einzelexemplaren auftauchten, war nicht in jedem Falle eine sichere Determination bis zur Art möglich. Werden diese zweifelhaften Formen, die in Abb. 1 nicht angeführt sind, mit berücksichtigt, so setzt sich der Artenbestand bereits im ersten Jahr aus etwa 20–25 Arten zusammen.

5 Jahren den Umfang annähernd vergleichbarer Gewässer erreicht hat, demonstriert die folgende Zusammenstellung:

| Autor | Gewässer | Trophiegrad | Untersuchungs-material | Probenzahl | Artenzahl |
|---|---|---|---|---|---|
| Wilbert (1969) | Weiher | eutroph | Aufwuchs | ca. 400 | 99 |
| Nusch (1970) | Vorbecken | oligotroph | Aufwuchs | ca. 100 | 46 |
| Nusch (1970) | Talsperre | oligotroph | Aufwuchs | ca. 100 | 21 |
| Nusch (1970) | Stauweiher | eutroph | Aufwuchs | ca. 200 | 64 |
| Obersee (1965—1969) | Weiher | oligotroph | Aufwuchs | 58 | 63 (1969) |

Wird die systematische Zugehörigkeit der neu hinzukommenden Arten betrachtet, so sind sowohl die Holotrichen als auch die Spirotrichen und Peritrichen von Anbeginn vertreten und der folgende Artenzuwachs erstreckt sich auf alle 3 Gruppen: nach unserem Material gibt es keine Verschiedenphasigkeit der Besiedlung durch einzelne systematische Gruppen.

Als der bemerkenswerteste Aspekt erweist sich jedoch, auf welche Weise sich die Ciliatenzönose entwickelt. Der Ciliatenbestand eines jeden Jahres geht weitgehend unverändert in der artenmäßigen Zusammensetzung in das nächste Jahr über. Und zu diesem Fundus gesellen sich die neu hinzukommenden Arten. Die Artendichte der Ciliaten wächst also, ohne daß es vorerst — betrachtet man längerfristige Zeitabschnitte, etwa wie hier die Jahreseinheiten — zu einer nennenswerten Sukzession kommt.

### *Die Wasserkäferzönose*

Im Gegensatz zu den Ciliaten unterliegt der Wasserkäferbestand erheblichen Schwankungen. Wie aus Abbildung 3 hervorgeht, sind von den im Jahre 1965 beobachteten 15 Arten im folgenden Jahr nur noch 8 vorhanden.

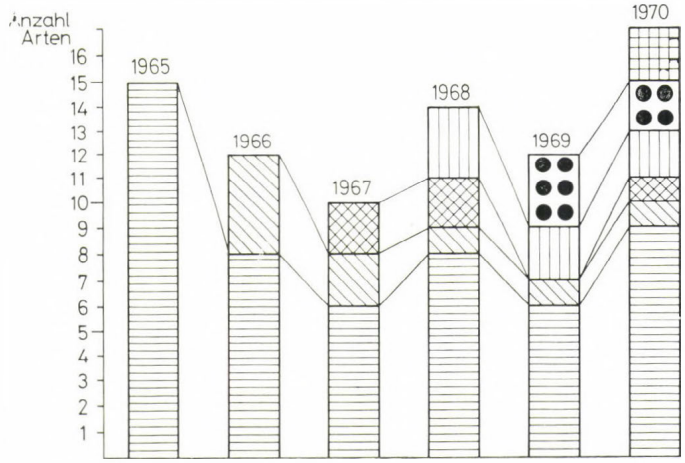


Abb. 3. Fluktuationsanalyse der Wasserkäferzönose im Obersee für die Jahre 1965 bis 1970. Weitere Erläuterung vgl. Abb. 2

Zwei Arten erscheinen im Jahre 1967 neu, sie werden auch 1968 nachgewiesen, fehlen aber im darauf folgenden Jahr. Wird die Präsenz der einzelnen Arten oder -gruppen analysiert (Abb. 4), dann verdichtet sich der Eindruck eines disharmonischen Käferbesatzes während der Initialphase.

In welch hohem Maße der Wasserkäferzönose in dem nun bereits 9jährigen Obersee immer noch Pioniercharakter zukommt, belegt eine Aufsammlung vom 14. August 1973. Die hierbei beobachtete Artenkombination [unterteilt in dominante (100—3% Abundanz), influente (3—1% Abundanz) und rezedente Arten (<1% Abundanz)] ist im folgenden aufgeführt:

| Art | Abundanz | Abundanz in % |
|---|---|---|
| 1. *Hyphydrus ovatus* L. | 96 | 66,7 |
| 2. *Noterus clavicornis* Deg. | 20 | 13,9 |
| 3. *Haliplus confinis* Steph. | 5 | 3,5 |
| 4. *Haliplus ruficollis* Deg. | 5 | 3,5 |
| 5. *Haliplus flavicollis* Strm. | 5 | 3,5 |
| 6. *Laccophilus minutus* L. | 3 | 2,1 |
| 7. *Enochrus testaceus* F. | 3 | 2,1 |
| 8. *Graptodytes pictus* F. | 2 | 1,4 |
| 9. *Haliplus obliquus* F. | 1 | 0,7 |
| 10. *Scarodytes halensis* F. | 1 | 0,7 |
| 11. *Potamonectes depressus elegans* Panz. | 1 | 0,7 |
| 12. *Hygrotus inaequalis* F. | 1 | 0,7 |
| 13. *Laccobius minutus* L. | 1 | 0,7 |

An der relativen Artenarmut, vor allem aber in der Eudominanz einer Art, von *Hyphydrus ovatus*, erweist sich die immer noch sehr instabile Käferbesiedlung. Einen noch einseitigeren Besatz beschreibt Koch (1972) für eine knapp $1^1/_2$jährige Kiesgrube (5 Arten, davon eine mit 89,6% eudominant).

Eine weitere Besonderheit stellen die geringen durchschnittlichen Individuenzahlen pro Ausbeute dar (13 Individuen/Ausbeute). Allerdings dürfte die spärliche Individuendichte nicht nur auf das geringe Alter des Obersees, sondern auch auf seinen anomalen Chemismus und die sich zunächst erst allmählich entwickelnde Makrophytenvegetation (vgl. Friedrich) zurückzuführen sein. Hiermit werden die Beobachtungen von Koch (1972) in vollem Umfange bestätigt, wonach sowohl zunehmende Wasserhärte als auch fehlender oder spärlicher Pflanzenwuchs in der Litoralzone die Besiedlungsdichte der Käfer vermindert.

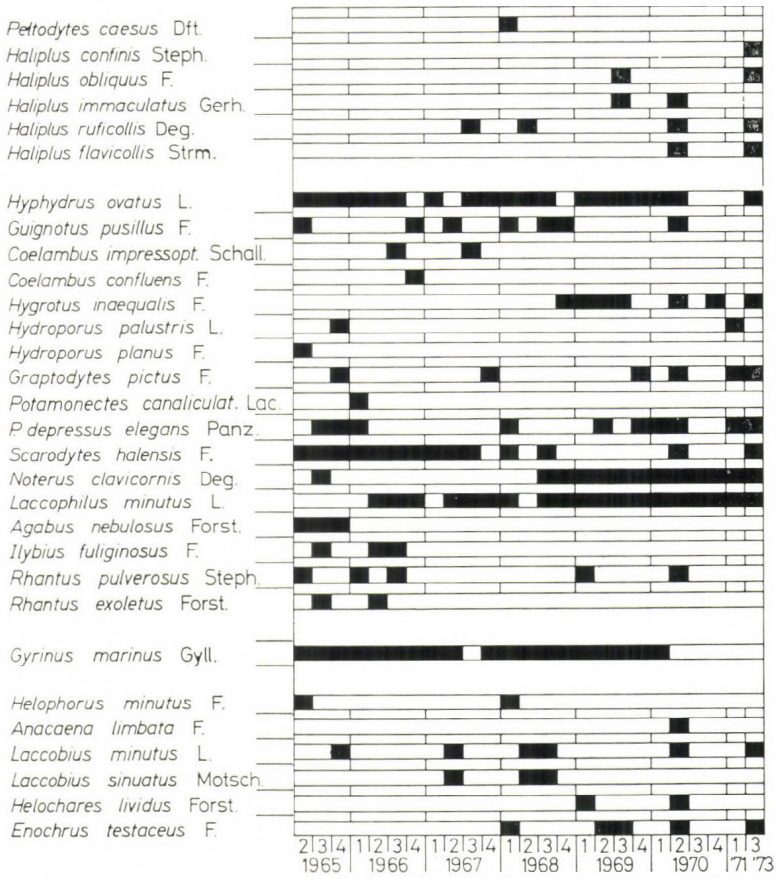


Abb. 4. Die zeitliche Verteilung der Wasserkäfer im Obersee

## DISKUSSION

Die Besiedlung eines neuentstandenen Gewässers ist—zumindest während der Initialphase—in großem Maße vom Zufall abhängig. Wenn trotzdem Ciliaten- und Wasserkäferzönose sich ganz unterschiedlich entwickeln, so ist nach den Ursachen hierfür zu fragen.

Von den dauernd in ein Gewässer eingetragenen encystierten Ciliaten treten schließlich nur diejenigen Arten in Erscheinung, die zusagende Lebensbedingungen vorfinden. Ändern sich diese Lebensbedingungen in einem Gewässer nicht grundlegend, so ist mit einer beträchtlichen Konstanz des Ciliatenbesatzes zu rechnen. Bereichert wird dieser Besatz lediglich durch diejenigen neu hinzukommenden Arten, die ebenfalls zusagende Milieubedingungen antreffen. Es ist auch naheliegend, daß in einem neuentstandenen Gewässer die »Zuwachsrate« zunächst recht hoch ist, sich mit zunehmendem Alter aber immer stärker abflacht (s. Abb. 2). Bei den sich meist durch gutes Flugvermögen auszeichnenden und daher aktiv die Gewässer aufsuchenden Wasserkäfern ist es dagegen durchaus möglich, daß einzelne

Arten zunächst Biotope besiedeln, in die sie nicht optimal eingepaßt sind. In neuentstandenen Gewässern ist das der Fall, wenn die biotopgemäßen Arten das Gewässer noch nicht besiedelt haben und die interspezifische Konkurrenz vorerst unterbleibt. Daher kommt es während der Initialphase zu erheblichen Fluktuationen innerhalb der Wasserkäferzönose.

Für die in diesem Zusammenhang wichtige Rolle des Faktors Zeit bei der Besiedlung eines Gewässers bietet auch der Obersee Beispiele. Herausgegriffen sei das gegenüber den Dytisciden, Gyriniden, Hydraeniden und Hydrophiliden verzögerte Auftreten der Halipliden. Die Halipliden tauchen ziemlich spät, nämlich erst im 3. Untersuchungsjahr auf (s. Abb. 4). Dies ist zweifellos eine Folge ihres geringen Flugvermögens, denn unzureichendes Nahrungsangebot scheidet als Ursache aus, da bereits im ersten Untersuchungsjahr *Tribonema*, *Mougeotia* und *Cladophora* als dichte Watten wuchsen (Friedrich). Darüber hinaus wies Seeger (1971) nach, daß ein großer Teil der Halipliden durchaus nicht auf fädige Grünalgen angewiesen ist, sondern animalische Kost bevorzugt oder zumindest annimmt.

Für zukünftige Prognosen über die Entwicklung von Zoozönosen in neuentstandenen Gewässern darf man nach den am Obersee gewonnenen Ergebnissen davon ausgehen, daß die Mikroorganismen in wenigen Jahren einen ausgewogenen und dem Charakter des Gewässers entsprechenden Bestand ausbilden. Für die Wasserkäfer, und diese Befunde darf man nach den vorliegenden Ergebnissen im Schrifttum wohl auf das gesamte Makrozoobenthos ausdehnen, gilt jedoch, daß über mehrere Jahrzehnte hin mit keiner ausgewogenen und stabilen Gemeinschaft zu rechnen ist.

## ZUSAMMENFASSUNG

Der Obersee, ein Braunkohlenrestgewässer, wurde vom Beginn der Füllung an 6 Jahre lang untersucht. Hoher Sulfatgehalt (bis 1080 mg/l) und entsprechend angewachsene Nichtkarbonathärte (bis 63 °d) sind die wichtigsten Kennzeichen des Gewässerchemismus. Die Entwicklung der Biozönose wird an 2 Organismengruppen, den Ciliaten und Wasserkäfern, demonstriert. Der Artenbestand an Aufwuchs-Ciliaten vergrößert sich kontinuierlich und nach 3 Jahren ist die Artendichte vergleichbarer Gewässer weitgehend erreicht. Demgegenüber entwickelt sich die Wasserkäferzönose sehr disharmonisch und weist auch nach 9 Jahren noch Pioniercharakter auf. Die Bildung eines ausgewogenen Makrozoobenthos in Braunkohlenrestgewässern währt mindestens mehrere Jahrzehnte.

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*Symp. Biol. Hung.*, *15*, pp. 273–279 (1975)

# OBSERVATIONS ON THE FISH PRODUCTION OF LAKE BALATON

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The shallow Lake Balaton has 596 km$^2$ water surface and its living space is about 1.8 km$^3$. Sebestyén (1967) has pointed out that 'Lake Balaton, in spite of its extensive surface, covers a relatively small body of water and the disproportionately long shore line renders it extremely sensitive to harmful external effects'. An incident supporting her statement was a mass fish kill in 1965 when about 500 tons of fish perished due to pesticide pollution. The fish fauna of Lake Balaton overcame this catastrophe but its far-reaching effects are still detectable.

In 1954, Entz tried to assess the production of the Lake in terms of Lindeman's energy levels. According to his statement, the fish from Lake Balaton are mostly harvested at their 3rd–4th years of age and as the annual catch approximates 2,000 tons, the biomass of nekton may be estimated at 6,000 tons. From these data, and from those referring to feeding, etc., the annual production of the total fish fauna of Lake Balaton may be assessed to be about 3,000 tons. At the level of fish or nekton — where the mean size of the organisms ranges from 40 mg to 80 kg — the average summer biomass is 10 g per m$^2$ increasing annually by its half (the final production may be estimated at 5 g per m$^2$).

The annual fish haul of Lake Balaton is relatively low. It varies between 1060 and 1963 tons. Fish fauna is represented by 44 species, but only 15–17 of them is of economic significance. Between 1950 and 1971, the annual catch of Lake Balaton changed between 17.5 and 32.9 kg per ha (Fig. 1). In 1950 and 1952, the yield per unit area generally increased, and then between 1952 and 1956 it decreased significantly. Since 1957, apart from small variances, the fish catch appears to be stabilized. Among predators the pike-perch (*Stizostedion lucioperca*) amounts to 6–12 per cent of the total 0.98–2.89 kg per ha. In 1950–1964 its yield increased from year to year, but in 1965 this value suddenly decreased to its one third. The volume of hauls increased again in the period 1965–1971 (Fig. 2). The fish kill in 1965 affected mostly the population of this predatory fish, because about 40 per cent of 500 tons of dead fish consisted of pike-perch.

Our detailed studies started in 1967 concentrated on pike-perch, the main predatory fish of Lake Balaton. We have studied its food (Biró 1973), growth (Biró 1970, 1972) and the age composition of the population, mortality, biomass, production and yield (Biró, MS).

Pike-perch in Lake Balaton turns to predation in its first year of age. Its fish consumption becomes general in the second year, but owing to an insufficient food supply the majority of them remains plankton-feeder. Conse-

quently, the age of recruitment to the predatory phase is 1+. The maximum age observed is 15+. Exploitation of the stock by fishing ranges from 3+ to 15+ year-old age groups, i.e. the economically important life span refers to 13 age groups. The majority of the catches is represented by 4+ year-old pike-perch in 56 per cent, about one-third of the catches is represented by 3+ year-old fish and the ratio of 5+ year-old specimens is about one-ninth of the total (Fig. 3).

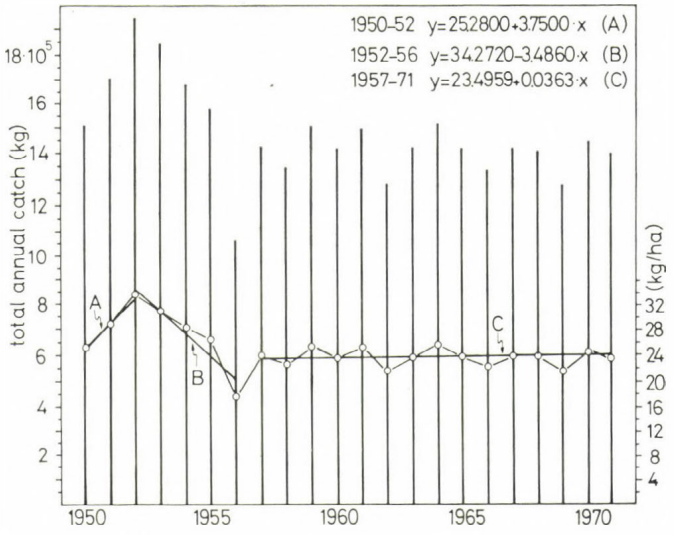


Fig. 1. Total annual fish hauls in Lake Balaton in kg (vertical lines) and in kg per ha (circles) during 1950–1971. *A*, *B* and *C* are the regressions expressing the mean catch per unit area (kg per ha) against the consecutive years

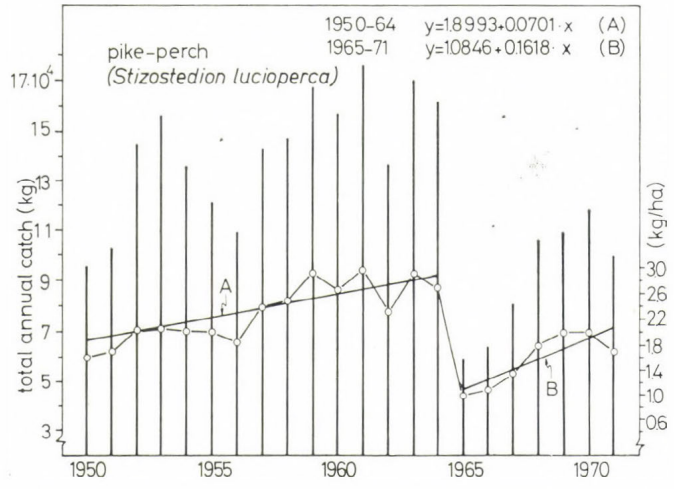


Fig. 2. Total annual hauls of pike-perch (*Stizostedion lucioperca* L.) in Lake Balaton during 1950–1971 (see also Fig. 1)

Fast and slow periods were distinguishable during the first summer growth of pike-perch fry in Lake Balaton (Biró 1972). Between June and August, presumably because of a change in feeding habit, the average growth became slow and then faster again. In September, after reaching 5.5–7.5 cm standard length, the growth almost stopped and practically there was no growth till the following spring. The growth rate of more than 3+ year-old pike-perch was found to be slow and uneven, too (Fig. 4). Pike-perch in Lake Balaton attains 1 kg body weight after its fifth year of life, i.e. both the length and weight increase is slow (Biró 1970).

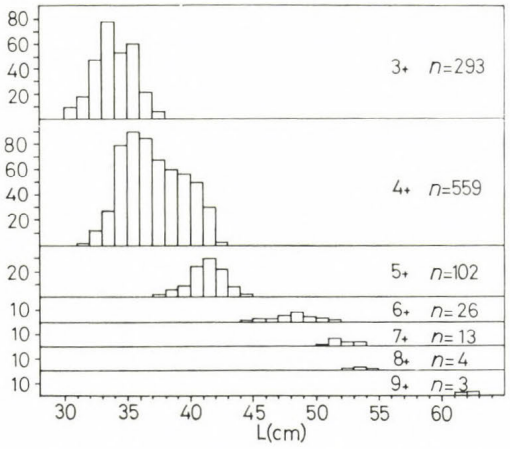


Fig. 3. Size-frequency histogram of pike-perch of different age groups examined for growth and age composition. $L$ = standard length in cm

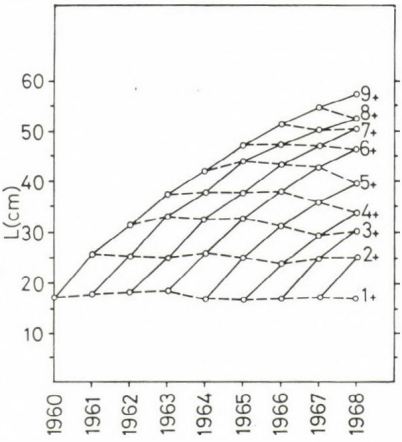


Fig. 4. Annual growth in length of pike-perch from 1+ to 9+ year-old age groups; lengths are back-calculated from scales

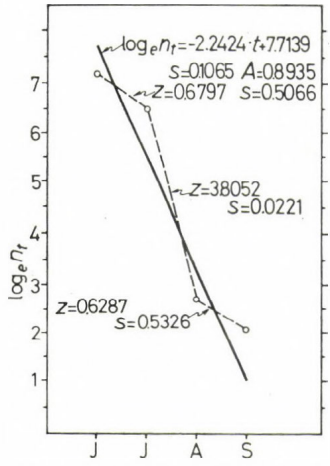


Fig. 5. Mortality of fry in the period of June to September. $n_t$ = number of fry in every $t$-period of time if $t$ = 1 month; $z$ = instantaneous total mortality coefficient; $s$ = coefficient of survival; $A$ = total annual mortality coefficient in this case referring to four months

The instantaneous mortality coefficient of fry was $z = 2.24$ from June to September (Fig. 5). The survival rate is $s = e^z = 11$ per cent. The average rate of mortality for the four summer months was 89 per cent. Decrease in the number of individuals during June–July, and later between August and September was lower, about 63–68 per cent, and accordingly, the survival rate was 51–53 per cent. In June and August, when a growth compensation was observed, mortality was predominant the survival rate being merely 2 per cent. As it can be seen, the rates are highly variable in the consecutive months. It is presumable that only 0.001–0.002 per cent of fry may reach

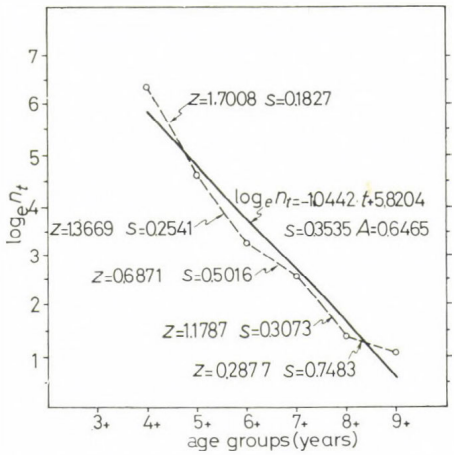


Fig. 6. Rates of mortality and survival in age groups from 3+ to 9+ (see also Fig. 5)

older age. For the part of population exploited by fishing, a rather high mortality rate was obtained ($z = 1.044,2$). The rate of survival was about 35 per cent ($s = 0.353,5$). Hence, the assessed value of the annual mortality was about 65 per cent ($A = 1 - s = 0.646,5$) for all age groups from 3+ to 9+. The survival rate fluctuated between 18 and 75 per cent, on the average 35 per cent, and the annual mortality between 25 and 82 per cent, on the average 65 per cent, resp. (Fig. 6).

Starting from back-calculated standard lengths and from specific weights (calculated by the length–weight relationship), we have received that the annual net production attains 50 per cent of the average biomass, according to the ratio $P/\bar{B} = 0.503,2$ (Fig. 7). The same value obtained from data on directly measured body length and weight proved to be about 49 per cent ($P/\bar{B} = 0.489,3$). The assessed rate of production is highest in the 3+ year-old age group (96 per cent), but it surprisingly decreases in the 4+ year-old group (27 per cent) as compared with the older fish. Loss in weight (negative production) was observed in the 9+ year-old age group of pike-perch. The gonad production is about 10 per cent of the total. During the first summer, the production of fry was 178 per cent ($P/\bar{B} = 1.785,2$). Production was highest in July–August, i.e. 253 per cent. From the middle of August to September this rate decreased from 88 to 30 per cent (Fig. 8).

The food of pike-perch consisted of 10–15 fish species. Among them 3–4 species are dominant, these being the bleak (*Alburnus alburnus*), pope

(*Acerina cernua*) and its own fry (*Stizostedion lucioperca*). In July and August, there usually is an intensive cannibalism. We found about 50 per cent of stomachs to be empty, from which we can conclude that there is insufficiency of food. In most cases the daily consumption varied between 1 and 4 g, the daily ratio being 0–1 per cent (Biró 1973).

For the estimation of food consumption and energy transformation of pike-perch we applied Winberg's (1956, 1961) balanced equation:

$$C = 1.25\ (Re + P)$$

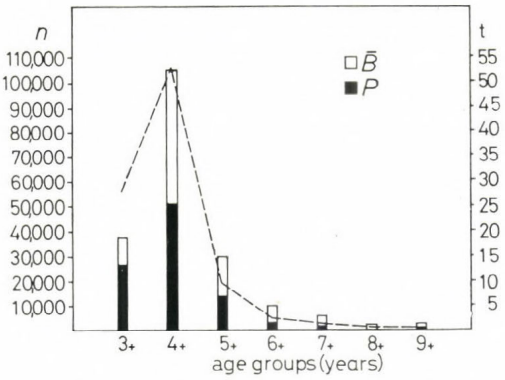


Fig. 7. Average biomass ($\bar{B}$) of age groups: 3+ to 9+, their annual production ($P$) in number ($n$) and in weight ($t$ = tons). Broken line means decrease in number of individuals, or mortality

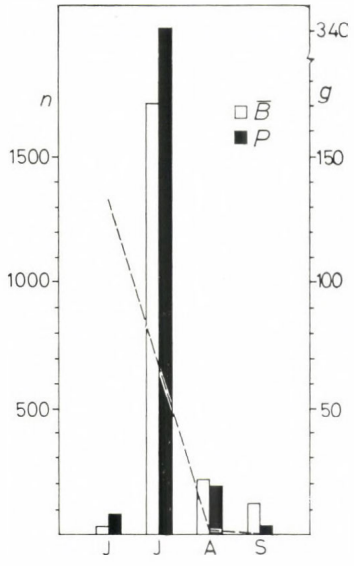


Fig. 8. Change of biomass ($\bar{B}$) and production ($P$) of one-summer-old pike-perch in number ($n$) and in weight (g) in the period from June to September

where $C$ = consumption; $Re$ = respiration (metabolism); $P$ = production. The relationship assumes that the metabolizable portion of ingested food is 80 per cent (20 per cent of the consumed food are excreta; urine and faeces: $U + Fe$). To assess the standard metabolism we have used the next formula according to Winberg (1956, 1961):

$$Re \text{ (ml } O_2 \text{ per h)} = 0.3\ w^{0.8}$$

where $w$ = weight of fish in g; $Re$ = respiration or standard metabolism at 20 °C. These values were calculated for the growing season (April–October) and for the period when pike-perch practically did not grow (November–March). The sum multiplied by 2 gave active metabolism (Winberg 1956, 1961, Mann 1965, Backiel 1971).

Projecting the calculated values to the whole surface of Lake Balaton we have received (Biró, MS) that:

$$C = 3.2 \text{ kcal/m}^2\text{/annum.}$$

Other parameters related to the mean consumption are:

— energy used for respiration:

$$Re = 0.8 \cdot C - P = 2.06 \text{ kcal/m}^2\text{/annum}$$

— energy lost as faeces and excreted materials:

$$(Fe + U) = 0.2 \cdot C = 0.64 \text{ kcal/m}^2\text{/annum}$$

— production of flesh and gonads:

$$P = 0.55 \text{ kcal/m}^2\text{/annum.}$$

Considering the predatory population as an open system in which the input is represented by food and recruitment and the output by fertilized eggs, yield, dead fish and metabolites (Backiel 1971):

$$P = C - (Fe + U + Re) = 0.5 \text{ kcal/m}^2\text{/annum.}$$

From this it follows that for a steady state of population in which the biomass instantaneously does not change ($B_1 = B_0$):

$$P + B_r = Y + B_m + B_e$$

where $B_r$ = biomass of recruits; $Y$ = yield; $B_m$ = biomass of mortality; $B_e$ = biomass of eggs shed. This equation for pike-perch in Lake Balaton in g per m$^2$ per annum values:

$$0.5 + 0.016 = 0.2 + 0.266 + 0.05$$

at $\bar{B} = 0.971 \pm 0.312$ g per m$^2$ per annum mean biomass value (the limits are 0.66–1.28 g per m$^2$). The biomass of dead fish can be calculated from the equation of steady state:

$$B_m = (P + B_r) - (Y + B_e) = 0.266 \text{ g per m}^2 \text{ per annum.}$$

This parameter is strongly influenced by the imperfectly known volume of sport fishing.

Replacing the production parameter ($P$) in the balanced epuation by its equivalent in terms of consumption and metabolism, the balanced equation of energy flow through the pike-perch population is the following:

$$\text{'Input'} \xrightarrow[\text{transformation}]{\text{energy}} \text{'Output'}$$

$$\begin{bmatrix} B_r + C \\ 16 + 3{,}200 \end{bmatrix} \rightarrow \begin{bmatrix} Y + B_m + B_e + (Fe + U) + R_e \\ 200 + 266 + 50 + \quad 640 \quad + 2{,}060 \end{bmatrix}$$

cal per m$^2$ per annum

$Re/C$ ratio shows the efficiency of energy dissipation by the system; it is 64.4 per cent. The ratio of $Be/C$ is the energy consumed for reproduction. It was about 1.56 per cent. The ratio of $Y/C$ was 6.25 per cent. The part of the consumed energy which returned to the ecosystem was $B_m + Fe + U$ per $C = 28.3$ per cent. Other indices are: $P/\bar{B} = 51.5$ per cent; $P/C = 15.6$ per cent and the ratio of $C/\bar{B} = 3.29$ per cent. On the basis of these parameters we can state that the consumed food has been transformed into fish body with significant loss: 64 per cent of the consumed food was utilized for respiration and about 15–16 per cent of it for production of flesh and gonads. Only about 1.56 per cent of energy consumed by the population was used annually for reproduction. Accuracy of all parameters calculated for the energy transformation of population is low because of wide variations.

Recently the organic production of plankton algae of Lake Balaton has been determined by Herodek (personal communication) and it was about 4.2 kcal per m$^2$ per day. In the period of vegetation calculated to the whole lake surface it was about $2.4 \times 10^9$ kcal per Balaton per day. Comparing the production of algae with those of the examined pike-perch population ($P = 0.55 \times 10^9$ kcal per Balaton per annum) it can be seen that only 0.001 part of organic material produced by plankton algae has been transformed to pike-perch flesh and gonads.

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# BIOLOGISCHE EIGENHEITEN DER GLAZIALEN HYDROFAUNA AUS DEN GEBIRGEN RILA UND PIRIN (BULGARIEN)

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Die Zahl der perennierenden stehenden Wasserbecken beläuft sich im Rilagebirge auf ungefähr 230 und im Piringebirge auf annähernd 165. Die Mehrzahl stellt Glazialseen dar, die zu jeweils 2 bis 11 in einem Kar gruppiert sind. Einzelne glaziale Seen sind in diesen Gebirgen eine Seltenheit.

Die Fläche der Gewässer schwankt zwischen 0,01 und 21,2 ha, wobei 70% 0,1 bis 1,5 ha aufweisen. Die maximalen Tiefen variieren zwischen 0,3 und 37,5 m, doch sind mit einer Tiefe über 5 m im Rila nur 12 und im Pirin 11 Seen bekannt. Tiefen von 1 bis 4 m sind vorherrschend (Ivanov u. Mitarb. 1964).

Die glazialen Wasserbecken des Rila- und Piringebirges sind im Höhengürtel von 1858 bis 2709 m gelegen, wobei die meisten zwischen 2 200 und 2 400 m ü.d. Meeresspiegel anzutreffen sind.

Gemäß ihrer Höhenlage, Tiefe und ihrem Durchfluß variiert das Temperaturregime erheblich. Bei den Seen mit einer Höhenlage bis zu 2 250 m bewegen sich die sommerlichen Oberflächentemperaturen um 12–13 °C, selten auch 20 °C. Bei den höher gelegenen übersteigt die Temperatur in der Regel nicht 10–11 °C, und bei den Seen, die einen Teil ihrer Eisdecke auch während des Sommers bewahren, sind in allen Schichten Wassertemperaturen von 4–7 °C zu verzeichnen.

Eine kompakte Eisdecke hält sich durchschnittlich 200–220 Tage im Jahre.

Die Sauerstoffmengen sind stets hoch (7,5–12 mg/l). Der pH schwankt zwischen 6,4 und 7,2. Die Gesamthärte ist gering (0,5–2,8 dH°); unbedeutend ist auch die Oxydierbarkeit (0,8–1,95 mg $O_2$/l).

Von besonderer Wichtigkeit sind die niederen Werte der Ca- und Gesamthärte, die sich auf die Populationsdichte aller Krebsartigen und Mollusken negativ auswirken, da zum Aufbau ihrer Panzer und Schalen das Kalzium notwendig ist. Eben darum können sich in den Gewässern am häufigsten und massenhaft Rotatorien (*Pedalia bulgarica*, mehrere *Synchaeta*-Arten, *Asplanchna* sp., *Conochilus unicornis*, *Polyarthra dolychoptera*) und *Chirocephalus diaphanus* von Branchiopoda, Anostraca entwickeln.

Der starke Durchfluß wirkt sich ungünstig auf die Planktonentwicklung aus und die kurze Vegetationsperiode (sowie die tiefen Temperaturen) reduzieren die Zyklen der Entomostraken.

In den von uns untersuchten 56 Seen (31 im Rila- und 25 im Piringebirge) wurden 41 Arten von Branchiopoden und Copepoden festgestellt (32 im Rila und 21 im Pirin), unter denen die Mehrzahl Litoral- oder Benthosformen sind. Wegen der schwachen Entwicklung einer höheren Wasservegetation sind phytophile Hydrobionten selten.

Das Plankton ist mit einer kleinen Artenzahl vertreten. Von den obenerwähnten Planktern treten am häufigsten und gelegentlich massenhaft *Daphnia hyalina, D. longispina, Eucyclops serrulatus* und *Chydorus sphaericus* auf.

Die Ermittlung der Verbreitung der Cladoceren und Copepoden in verschiedenen Höhenlagen zeigt, daß der überwiegende Teil die Zone über 2000 m ü. d. M. besiedelt (Abb. 1) und ein viel kleinerer Teil typische Besiedler der Niederungen sind (unter 1 800 m wurden tektonische Wasserbassins erforscht). Als echte Bewohner der alpinen Stufe im Rila- und Piringebirge

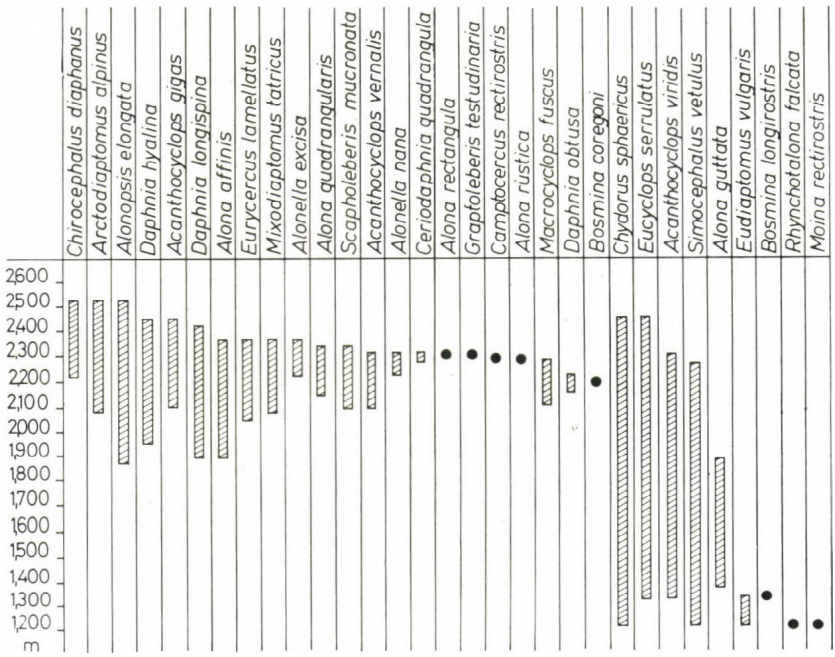


Abb. 1. Vertikale Verbreitung der Entomostraken im Rila- und im Piringebirge

sind *Alonopsis elongata, Megacyclops gigas, Camptocercus rectirostris* und *Arctodiaptomus niethammeri* zu erwähnen und gelegentlich *Mixodiaptomus tatricus* und *Alona rustica*. Die übrigen Arten sind eurytop, so daß ihre Verbreitung im Gürtel 1 900–2 500 m durch andere Faktoren und nicht von der Höhenlage und dem glazialen Ursprung der Wasserbecken bedingt ist.

Besonderes faunistisches und ökologisches Interesse gilt *Chirocephalus diaphanus*, der einerseits glaziale Gewässer über 2 000 m Höhe besiedelt und andererseits in der Donauebene und in Thrakien ziemlich verbreitet ist. Versuche einer morphologischen Abgrenzung der Hochgebirgspopulationen von jenen des Tieflandes verliefen bis jetzt erfolglos.

Mit Ausnahme von *Mixodiaptomus tatricus* werden alle für die alpine Stufe des Rila- und Piringebirges charakteristischen Arten in den Wasserbassins der Niederungen angetroffen, die vornehmlich eiszeitlichen Ursprungs von Zen-

tral- und Nordeuropa sind. *Arctodiaptomus niethammeri* ist von den Steppen Kleinasiens, dem Unterlauf des Don und aus dem Peristergebirge in Mazedonien bekannt (Flössner 1964, Naidenow 1970, Kiefer 1971).

Beim Vergleich der Faunenliste der Pirin- (Naidenow 1968) und Rilagewässer macht die erstaunliche Ähnlichkeit der Leitformen unzweifelhaft Eindruck. Die größere Anzahl der im Rilagebirge bekannten Entomostraken ist in hohem Ausmaß auf das Vorhandensein vieler Seen und Tümpel im Waldgürtel zurückzuführen, Biotope, die im Piringebirge fast gänzlich fehlen.

Ein wesentlicher Unterschied zwischen den Seen der bei den Gebirgssysteme besteht im Vorhandensein von *Bosmina coregoni* im Rila, die aus vielen Gewässern der Alpen, Karpaten und der Tatra bekannt ist. In beiden bulgarischen Gebirgen fehlen Vertreter der Gattung *Cyclops* sowie *Acanthodiaptomus denticornis* und *Holopedium gibberum*, die in den Seen der Alpen und der Tatra ziemlich verbreitet sind.

Die Hochgebirgsseen Bulgariens müssen nach ihren hydrologischen, hydrochemischen und hydrobiologischen Eigenheiten dem oligotrophen Typus zugeordnet werden. Der Grad der Oligotrophie schwankt jedoch in ziemlich breiten Grenzen, in Abhängigkeit vom Alter, dem Terrain und der Höhenlage.

Die geologisch jüngsten Seen sind am höchsten gelegen. Das Seebecken und seine Ufer werden von großen Felsenstücken gebildet, der Durchfluß ist sehr stark, Grundablagerungen fehlen, die Versickerung ist erheblich. Die Sauerstoffsättigung beträgt in sämtlichen Schichten etwa 100%, und die in das Wasser gelangenden organischen Stoffe werden in kurzer Zeit vollkommen abgebaut. Die Schwankungen des Wasserspiegels sind beträchtlich. Bei Schneeschmelze und reichlichen Regenfällen steigt ihr Seespiegel rasch um 1–3 m an, fällt aber nachher auch rasch wieder ab, da das Wasser zwischen den Felsenbrocken versickert.

Das Zooplankton dieser Seen ist qualitativ und quantitativ außerordentlich arm. Netzphytoplankton fehlt in der Regel. Das Pelagial ist nur von *Daphnia hyalina* und *Megacyclops gigas* besiedelt und in den am Ufer gelegenen Zonen wird auch *Chydorus sphaericus*, *Alonopsis elongata*, *Eucyclops serrulatus* und manchmal *Chirocephalus diaphanus* angetroffen. Aus Mangel an Grundablagerungen entwickelt sich kein Benthos.

Das zweite Stadium im Leben der glazialen Seen wird durch die Ablagerung einer dünnen Schlammschicht charakterisiert, die eine Abflußverminderung durch Einschränkung der Versickerung und schließlich eine Verstärkung der Mineralisation zur Folge hat. Alljährlich wird eine Entwicklung vom Phyto- und Zooplankton, wenn auch in kleinen Mengen, beobachtet. Außer den zum ersten Entwicklungsstadium gehörenden Komponenten, werden zusätzlich noch *Daphnia longispina*, einige Arten Alona, *Acanthocyclops vernalis* (s. str.), *A. viridis* u. a. angetroffen. Das Benthal wird mit Insektenlarven und Würmern besiedelt, die gewöhnlich geringe Dichte aufweisen. Reicheres Leben besitzt die Zone des Seeabflusses. Die zerstörten Felsenstücke bilden eine flache und enge sand-kiesige Litoralzone, in der sich Hydrophyten ansiedeln, die bei jeder Vereisung des Sees vernichtet werden.

Zu dieser Kategorie gehört die Mehrzahl der Seen des Rila- und Piringebirges.

Das dritte Stadium wird durch mächtige mineralische und organische Ablagerungen gekennzeichnet. Das Sauerstoffregime im Epilimnion ist gün-

stig, aber dem Grunde zu fällt die Sättigung manchmal bis zu 30% ab, so daß eine völlige Oxydation der organischen Stoffe nicht eintritt. Während des größeren Teils des Jahres ist reichliche Chrysophyceen- und Kieselalgenentwicklung vorhanden. Verhältnismäßig reich ist auch das Zooplankton, vertreten durch *Daphnia hyalina*, *D. longispina*, *Keratella cochlearis*, Copepoditen von Cyclopoida und *Mixodiaptomus tatricus*. Quantitativ herrschen die Entomostraken vor.

Die Seeufer von dieser Kategorie sind stark vergrast, das Eulitoral mit harter Wasservegetation bewachsen. Die emersen Pflanzen bedecken manchmal einen erheblichen Teil der Seeoberfläche. Es entwickelt sich ein spezifischer litoraler psammo-phytophiler faunistischer Komplex, in dem *Alonopsis elongata* dominiert.

Das vierte Stadium umfaßt die Periode des Versumpfens und der Eutrophierung der Seen bis zur Umwandlung in Moraste oder feuchte Seeterrassen. Anfangs drückt sich dieser Prozeß durch intensive Ablagerung von Schwemmland aus, durch ein schnelles Seichtwerden des Sees und Vorrücken der Wasservegetation zur Seemitte. Die pelagischen Planktonorganismen nehmen ab, um letztlich völlig zu verschwinden. Infolge der reichen Entwicklung der Sphagnaceen wird das Wasser saurer (pH ca. 6,5), was zu einer Abnahme der Abbauprozesse führt. In dieser Etappe sterben die Fische und Eulimnobionten aus, oder sie emigrieren nach Möglichkeit in benachbarte günstigere Bassins. In der Endphase wird die ganze Oberfläche mit sauren Gräsern und Moosen bedeckt, womit das limnische Leben erlischt.

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*Symp. Biol. Hung.*, *15*, pp. 285–295 (1975)

# PARTICIPATION OF BACTERIA *DAPHNIA PULEX* AND *ALBURNUS ALBIDUS ALBORELLA* IN THE ORGANIC PRODUCTION OF LAKE OHRID

by

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The organic production of the fresh-water ecosystems is of primary importance concerning the structure of their living communities.

This study, discussing the participation of the bacterioplankton *Daphnia pulex* and *Alburnus albidus alborella* in the organic production of Lake Ohrid, will clarify at least one link in the giant complex of interacting relationships in this biotope.

## MICROBIOLOGICAL RESEARCHES

Bacterial community of the lake water, as an integral part of planktonic community, plays an important role in the complex chain of nutrition. The small dimensions enable the microorganisms to perform intensive metabolism with the successive accumulation of high-quality nutrients. The bacterioplankton being rich in high-calorie nutrients and indispensable vitamins is an ideal source of food for filter-feeders (Cladocera, Copepoda).

Bacterioplankton as food source for zooplankton in Lake Ohrid is the subject of the present investigations.

Bacterioplankton in Lake Ohrid is found from the surface down to the greatest dephts (for methods and material see Ocevski 1966). Larger quantities of bacterioplankton were found in the upper trophic layer from 0 m to a depth of 50 m. The quantities of heterotrophic bacterioplankton in the pelagial zone of Lake Ohrid from the surface (0 to 1 m) to a depth of 50 m in the period 1966 to 1969 are given in Table 1.

The number of planktonic bacteria (Table 1) varied between 12 and 28,550 per ml. Two maxima have been found, one in the surface layers (0 to 10 m) and one at 50 m. In the layers from 20 m to a depth of 40 m where zooplankton is maximal, the heterotrophic bacterioplankton is minimal.

The intestinal content of *Daphnia pulex* collected in this lake was composed of rod-shaped, azotobacter-like and coccal bacteria, yeast-like cells and planktonic algae (Table 2).

Table 2 illustrates that the rod-shaped and azotobacter-like bacteria dominate in the intestinal content, followed by the yeast-like cells, planktonic algae and bacteria.

The significance of the relationship between the fauna of the lakes and their bacterial population is emphasized by Baier (1935) who points out the importance of bacterioplankton as food for water animals. Also the importance of bacteria in the nutrition of *Daphnia* is stressed by Gayevskaya (1938) and Rodina (1964).

TABLE 1

*Vertical distribution of heterotrophic bacterioplankton in the period from 1966 to 1969 (number per ml of water)*

| Depth in m | Febr. 1966 | May 1966 | Aug. 1966 | Sept. 1966 |
|---|---|---|---|---|
| 0 to 1 | 747 | 2,820 | 1,200 | 305 |
| 10 | 1,285 | 1,765 | 1,430 | 204 |
| 20 | 3,735 | 643 | 1,120 | 183 |
| 30 | 2,925 | 1,100 | 810 | 219 |
| 40 | 2,975 | 890 | 664 | 870 |
| 50 | 5,770 | 1,930 | 124 | 705 |
| | Febr. 1967 | May 1967 | Aug. 1967 | Oct. 1967 |
| 0 to 1 | 4,190 | 3,010 | 400 | 524 |
| 10 | 1,910 | 48 | 1,500 | 798 |
| 20 | 622 | 47 | 50 | 290 |
| 30 | 350 | 113 | 46 | 80 |
| 40 | 2,075 | 315 | 70 | 138 |
| 50 | 661 | 530 | 12 | 405 |
| | Febr. 1968 | May 1968 | Aug. 1968 | Oct. 1968 |
| 0 to 1 | 138 | 700 | 388 | 4,980 |
| 10 | 109 | 23,700 | 139 | 3,600 |
| 20 | 108 | 1,054 | 243 | 456 |
| 30 | 152 | 456 | 131 | 21 |
| 40 | 118 | 317 | 32 | 207 |
| 50 | 61 | 282 | 13,925 | 2,885 |
| | Febr. 1969 | March 1969. | June 1969 | Oct. 1969 |
| 0 to 1 | 344 | 286 | 2,780 | 490 |
| 10 | 28,550 | 95 | 2,760 | 300 |
| 20 | 985 | 78 | 830 | 139 |
| 30 | 2,695 | 58 | 286 | 167 |
| 40 | 4,820 | 66 | 154 | 30 |
| 50 | 19,270 | 1,250 | 6,827 | 435 |

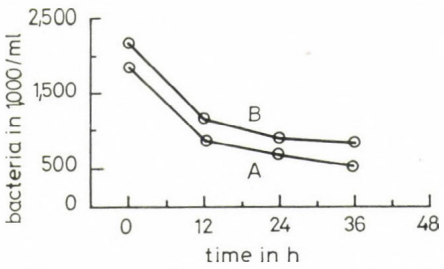


Fig. 1. Rate (1,000 per ml/h) of utilization of bacteria as food by *Daphnia pulex* (experimental study). A = cocci from bacteria; B = rod-shaped bacteria

TABLE 2

*Composition of the intestinal content of Daphnia pulex (evidenced by microscope)*

| Date | | Bacteria | | | Other microorganisms | |
|---|---|---|---|---|---|---|
| | | 1. rods | 2. cocci | 3. azotobacter-like | 1. yeast-like | 2. algae |
| 16. 10. 68 | D1 | +++++ | +++−− | ++++− | ++−−− | +−−−− |
| | D3 | +++++ | +++−− | +++++ | ++−−− | ++−−− |
| | D5 | +++++ | +−−−− | +++++ | +++−− | −−−−− |
| | D7 | ++++− | ++−−− | ++++− | +++++ | −−−−− |
| | D9 | ++++− | +−−−− | +++++ | ++−−− | +−−−− |
| 19. 2. 69 | D1 | +++++ | +++−− | +++−− | +−−−− | +++−− |
| | D3 | ++++− | +++++ | ++−−− | +−−−− | ++−−− |
| | D5 | +++−− | +++−− | ++−−− | +++−− | ++−−− |
| | D7 | ++++− | ++−−− | +++−− | +++−− | ++−−− |
| | D9 | ++++− | ++−−− | −−−−− | +−−−− | +−−−− |
| 19. 6. 69 | D1 | +++++ | ++−−− | ++++− | +++−− | +++−− |
| | D3 | +++++ | +++−− | +++−− | +++−− | ++−−− |
| | D5 | +++++ | +++−− | +++++ | +++−− | ++−−− |
| | D7 | +++++ | ++−−− | ++++− | +++−− | ++−−− |

+ + + + +: present in the greatest number; + + + + −: present in a great number; + + + − −: present in the mean numbers; + + − − −: present; + − − − −: present in a small number; − − − − −: not present

Consequently, the experiments were performed by using bacterioplankton isolated from Lake Ohrid, as food by *Daphnia pulex*. Thus, on the basis of our laboratory experiments, the numerous dissections of *Daphnia* and the microscopical observations of its intestinal contents, it can be concluded that bacteria are ingested and digested by crustacean zooplankton. In our investigations with suspensions of cocci-shaped bacteria the maximum values of their ingestion by *Daphnia pulex* were 5.74 per cent in the first 12 hours; in the subsequent 12 hours it used only 1.03, and in the last 12 hours 0.39 per cent; the total for 36 hours was 7.16 per cent per animal (Fig. 1A).

Suspension of rod-shaped bacteria was utilized to a lesser extent by the experimental animals in the 36-hour period. So in the first 12 hours bacteria were ingested by *Daphnia* in 4.09 per cent, but in the next 12 hours the rate of utilizing rod-shaped bacteria decreased to 1.03, and in the last 12 hours to 0.33 per cent (Fig. 1B), or more exactly, for the 36-hour period every experimental filter feeder utilized 6.07 per cent.

For this reason, the density of the bacterioplankton in Lake Ohrid is more or less dependent on the abundance of bacteria and on their utilization in the food cycles as filter feeders.

## STUDIES ON ZOOPLANKTON

Although *D. pulex* is numerically not the dominant species of the planktonic community owing to its biomass, it is the most significant element.

Investigations of the two Ohrid salmonids *Salmo letnica* Kar., and *Salmothymus ochridanus* (Steindachner) (Stefanović 1948, Hadžišče, un-

TABLE 3

*Fluctuation of number of D. pulex in groups of different length in 1966 (absolute values)*

| Date | Free eggs | Free embryos | Length groups (length in μ) ♀♀ without eggs | | | | | | | | | | ♀♀ with eggs | | | | | Total (eggs, embryos), young and grown ♀♀ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 525–700 μ | 700–875 μ | 875–1,050 μ | 1050–1,225 μ | 1,225–1,400 μ | 1,400–1,575 μ | 1,575–1,750 μ | 1,700–1,925 μ | 1,925–2,100 μ | 2,100–2,275 μ | 1,400–1,575 μ | 1,575–1,750 μ | 1,750–1,925 μ | 1,925–2,100 μ | 2,100–2,275 μ | |
| 22. 2. 66 | — | — | — | — | — | 2 | 2 | 5 | 26 | 25 | 28 | — | — | — | 2 | 1 | — | 91 |
| 2. 3. | — | — | — | — | 2 | — | — | 7 | 27 | 17 | 3 | — | — | — | 6 | 3 | — | 65 |
| 11. 3. | 1 | — | 11 | 10 | 3 | — | 3 | 2 | 58 | 15 | 14 | — | — | 2 | 22 | 11 | — | 152 |
| 21. 3. | 1 | 3 | 43 | 12 | 13 | — | — | — | 8 | 38 | 16 | — | — | 1 | 18 | 9 | 1 | 168 |
| 2. 4. | — | — | 39 | 35 | — | 5 | — | — | 3 | 31 | 1 | — | — | 2 | 10 | 9 | — | 135 |
| 5. 4. | — | — | 12 | 34 | 14 | 5 | 2 | — | 7 | 49 | 5 | — | — | — | 17 | 13 | — | 158 |
| 12. 4. | 1 | — | 21 | 12 | 30 | 32 | 8 | 4 | 5 | 28 | — | — | — | — | 11 | 5 | 3 | 160 |
| 16. 4. | 1 | 1 | 44 | 14 | 14 | 7 | 6 | 5 | — | 12 | 6 | — | — | — | 11 | 3 | — | 124 |
| 20. 4. | — | — | 18 | 10 | 8 | 21 | 3 | 10 | 14 | 7 | — | — | — | — | 5 | 4 | — | 100 |
| 25. 4. | — | 1 | 1 | 33 | 22 | 21 | 54 | 13 | 20 | 21 | 19 | — | — | — | 16 | 10 | 2 | 233 |
| 30. 4. | — | 4 | 2 | 10 | 14 | — | 14 | 44 | 15 | 10 | 2 | — | — | — | 7 | 11 | — | 133 |
| 7. 5. | — | — | 1 | — | 21 | 20 | 19 | 30 | 13 | — | — | — | 1 | 4 | 8 | 3 | — | 120 |
| 21. 5. | 3 | 6 | 4 | 45 | 28 | 15 | 12 | 18 | 14 | 8 | 2 | — | — | 4 | 8 | 7 | — | 174 |
| 1. 6. | 1 | — | 6 | 38 | 36 | 25 | 24 | 21 | 17 | 5 | 2 | 2 | — | 9 | 9 | 3 | — | 198 |
| 11. 6. | 5 | 1 | — | 29 | 65 | 19 | 31 | 52 | 23 | 7 | — | — | — | 7 | 9 | 1 | 1 | 250 |
| 24. 6. | 2 | 4 | 228 | 128 | 88 | 28 | 49 | 151 | 40 | 4 | 5 | 1 | 1 | 23 | 24 | 11 | 1 | 788 |
| 5. 7. | 2 | — | 347 | 225 | 82 | 51 | 42 | 52 | 103 | 35 | 7 | — | — | 15 | 31 | 6 | — | 988 |
| 14. 7. | 1 | 14 | 447 | 326 | 216 | 29 | 22 | 50 | 66 | 19 | 9 | 9 | — | 10 | 12 | 2 | — | 1,252 |
| 23. 7. | 6 | 5 | 524 | 386 | 314 | 240 | 283 | 49 | 26 | 20 | 24 | 1 | — | 13 | 11 | 7 | — | 1,909 |
| 8. 8. | 9 | 7 | 382 | 446 | 361 | 266 | 157 | 56 | 70 | 8 | — | — | 4 | 15 | 11 | — | — | 1,792 |
| 12. 8. | 3 | 5 | 315 | 384 | 269 | 165 | 143 | 245 | 123 | 67 | 19 | — | — | 29 | 20 | 4 | — | 1,791 |
| 22. 8. | 4 | 6 | 322 | 291 | 289 | 164 | 113 | 219 | 180 | 23 | 2 | — | 2 | 21 | 19 | 3 | — | 1,658 |
| 31. 8. | — | 14 | 313 | 264 | 289 | 162 | 202 | 148 | 232 | 40 | — | — | 1 | 9 | 17 | 7 | — | 1,698 |
| 2. 9. | 6 | 16 | 313 | 327 | 181 | 283 | 219 | 181 | 185 | 148 | 45 | 6 | — | 19 | 19 | 2 | — | 1,950 |
| 10. 9. | 7 | 8 | 435 | 158 | 230 | 137 | 258 | 395 | 264 | 91 | 14 | — | 4 | 12 | 26 | 6 | 1 | 2,046 |
| 22. 9. | 2 | 7 | 85 | 253 | 141 | 133 | 187 | 394 | 395 | 56 | 9 | — | 1 | 10 | 25 | 8 | 3 | 1,709 |
| 4. 10. | 3 | 1 | 11 | 51 | 72 | 258 | 362 | 815 | 486 | 151 | 13 | 1 | — | 7 | 16 | 2 | 1 | 2,250 |
| 17. 10. | — | — | — | — | 7 | 30 | 82 | 207 | 374 | 147 | 16 | 2 | — | — | 5 | — | — | 870 |
| 29. 10. | 2 | 1 | — | — | 9 | 9 | 52 | 234 | 407 | 82 | 1 | — | — | 4 | 8 | 2 | — | 811 |
| 22. 11. | — | 2 | — | — | — | 24 | 11 | 70 | 189 | 27 | 5 | 1 | — | — | 1 | 5 | 1 | 335 |
| 2. 12. | — | — | — | 8 | 7 | 16 | 28 | 23 | 101 | 96 | 2 | — | — | 9 | 8 | 2 | — | 200 |
| 28. 12. | — | — | — | — | 3 | — | 8 | 6 | 4 | 21 | 5 | — | — | — | 4 | 2 | — | 53 |
| 7. 1. 67 | — | — | — | — | — | 6 | — | 6 | 19 | 43 | 11 | — | — | — | 5 | — | — | 90 |

published data) and cyprinids (Točko 1969) showed that *D. pulex* is of primary importance in the nutrition of these species.

It is well-known that *D. pulex* lives in ponds and is to be found in the littoral of great lakes. Since the species is found throughout the year in the pelagial region of Lake Ohrid it is worthwhile to study its biology and ecology. This species was collected between 1965 and 1968 at intervals of ten, frequently of seven or even three days (Table 3).

In January and February single specimens of large, old individuals can be found in the plankton of the lake. Their number does not exceed 5 ind. per $m^3$ of water. Some of them probably carry abortive eggs. With certain oscillations the population of *Daphnia* subsists in March and in the first half of April, mainly represented by aged growth classes. In the last decade of March part of the old individuals produces the new generation and now the population is composed chiefly of young females. The temperature enhances intensive growth and early maturation so that in the subsequent days the middle-aged growth classes, i.e. individuals from 700 to 1,750 $\mu$ are dominant. These are all young females having just reached sexual maturity, more than 70 per cent carrying 1 or 2 eggs; thirty-six per cent of all females carrying egg has only a single one.

Such a population structure leads to an intensive reproduction which results in an increase of the population in general and the domination of the young classes. In the last ten days of April, 43 per cent of the total population is represented by length classes II, III and IV, and 57 per cent by classes V, VI and VII, whereas the older and larger specimens are absent from the plankton. Although the temperature of water layers in which the *Daphnia* lives is not high, ranging from 13.38 °C to 6.45 °C, the growth is intensive, molting occurs at short intervals, and in May the total population is composed of adult females but young growth classes, which means that we have completely new, i.e. renewed population, in the phase of intensive reproduction.

June, July, August, September and the first ten days of October are the period of maximum population density of *D. pulex* being at the same time the period of intensive reproduction. High temperatures varying from 20.94 °C to 6.98 °C in July; from 22.30 °C to 6.80 °C in August; from 21.80 °C to 6.91 °C in September; from 19.65 °C to 6.86 °C in the first ten days of October, and abundance of food (phytoplankton or bacteria) help fast transformation of certain stages, egg maturation and embryonic growth, resulting in the great dynamics in the population composition of *D. pulex*. The total population gradually increases but the ratio of the young to sexually mature individuals is always different.

From the second decade of October the decrease of *Daphnia* population, the diminishing of reproduction, the gradual disappearance of young growth classes, a permanent increase of old classes begin but with a considerable decrease in the total population reaching the lowest point in December and January. The population is mainly composed of large, old individuals, some of them carrying one egg which, most probably, is abortive since we had not been able to find young individuals in the plankton.

In order to analyse its population dynamics throughout the year monthly measurements of *D. pulex* from the collected material were performed. Thus the length classes of the newborn specimens and those of the sexually mature

and the old females were determined. Division of *Daphnia* in different length classes enables us to determine the growth, sexual maturation, age distribution, dying rate and the life span of *D. pulex* in the lake.

Ten groups were differentiated, four of them representing young, sexually immature individuals, and the other six sexually mature *Daphnia* (Meškova 1952).

The newborn individuals of *D. pulex* are (from the top of the head to the beginning of the spine) 525 to 700 $\mu$ long. Between 1,225 and 1,400 $\mu$ they are young and sexually immature. The size of the sexually mature individuals varies from 1,400 to 2,100 $\mu$. Many of the individuals over 1,925 $\mu$ do not multiply and are old. The few specimens from 2,100 to 2,275 $\mu$ are very old.

Analyses of the measurements show the following dynamics: in January length class VIII dominates in the plankton of Lake Ohrid being followed by classes VII and IX, represented approximately by the same values. Classes VI and V are represented only by single specimens. Young individuals do not occur at all.

In February, with a decrease in the total population, length class IX predominates, i.e. the dominating class from the previous month which continued growing. Immediately after it follow classes VIII and VII. Classes VI, V and IV are represented by low values.

In March, there is an increase in the absolute number of class VIII owing to the transformation of the individuals belonging to class VII of the previous month.

In the first ten days of April, since reproduction has begun during March, young classes appear and dominate. The most common are classes I and II, and also a special grouping around class VIII is obvious. Old individuals of class X cannot be encountered in the plankton at all.

May is the period of young populations with the domination of the representatives of length class II, followed by classes III, IV, V and VI.

In June, parallel to the growth of the total population, intensive growth and molting can be observed. Class VI dominates followed by classes V and VII. New generations belonging to classes I, II, III and IV are highly perceivable.

In July all the growth classes (from the youngest to the oldest) and all length classes (from the shortest to the longest) are present. Class I dominates, after it come classes II, III, IV and V observed at the end of June. But at the same time, the intensive reproduction of the middle-aged classes continues resulting in the increased importance of classes III and IV, in the last ten days of July.

In August the same situation can be observed. A great percentage of females lays eggs, resulting in the appearance of the new young generation at the beginning of September, however, in smaller numbers than in July.

At the end of September, classes VI and VII dominate represented by almost the same values; classes V, IV and III occur in a considerably smaller number, but classes II and VIII are still rarer, while classes I and IX are represented by a few specimens.

In October, length classes VI and VII dominate, and there is a regular grouping around them of the other classes. Length classes I, II, III are absent, but very large, old individuals of class X are found.

In November, the total population decreases. Like in the previous months, class VII dominated, followed by classes VI, V, VIII, IV and IX. Single specimens of class X were also found.

Finally, in December, the population goes on decreasing. In this period length class VIII is dominant, while classes VII, VI, V, and IX are represented by single specimens.

From the above analyses it can be concluded that in Lake Ohrid three generations of *D. pulex* population occurs in a year. *Daphnia* born in March and April, multiplying in April, May and in the first part of June dies in July. *Daphnia* born in May and June multiplying in July, dies in the second part of August and in September. Finally, *Daphnia* born in July and in the first part of August, multiplying in August and September dies in November, December and January.

So the average length of life of *D. pulex* in Lake Ohrid is about 110 days.

## ICHTHYOLOGICAL STUDIES

Ohrid bleak *Alburnus albidus alborella* Filippi is a significant member of the ichthyo-fauna of Lake Ohrid and of the whole lake ecosystem (Točko 1967). For several years its annual catch came just after that of the noblest fish of the lake and amounted to a quarter of the total catch (Stanković 1960, Točko 1967). With regard to this it can be compared with Prespa bleak (*Alburnus alburnus belvica* Karaman) and Skadar bleak inhabiting Lake Skadar (Točko 1959, Ivanović 1964).

Ohrid bleak inhabits the littoral of the lake [from 0 to 18 (20) m] where life conditions are the most diverse and most variable. Its shoals can be rarely found in other regions of the lake. It is obvious, nevertheless, that there is a certain differentiation in the composition of its shoals and of the total population in common. It can be certainly divided into three main categories: 1. shoals of larvae and of young individuals, several months old which, as a rule, live over a somewhat extensive zone of Cladophora or near the surface of the upper littoral (0 to 5 m); 2. shoals composed of young individuals aged 1 to 2 years, living in the upper littoral of the lake, too, isolated from the shoals of the previous category; 3. shoals of adults, many of them reaching over 10 m in length.

Unlike the Ohrid bleak, Skadar bleak and Prespa bleak also grouped in relatively large and numerous shouls, move and live throughout the whole lake inhabiting its pelagial, too.

Shoals of Ohrid bleak subsist even during sexual activity, from the middle of May up to the beginning of August, but with considerable changes. In this phase, the sexually developed specimens go in the upper and shallow littoral of the lake grouped in shoals of several individuals, predominantly males, arranged closely one by one giving the impression of a large scattered shoal from the vegetative stage.

Ohrid bleak spawns along the extensive zone of Cladophora at a depth from 0.5 to about 2 m and, very rarely, its sexually developed individuals go down along the chara-prairies spawning at the depth of 10 to 12 m which is, undoubtedly, an ecological characteristic of the population of Ohrid bleak.

The spawns of Ohrid bleak are already developed and eyed eggs are relatively small with a diameter of about 1.5 mm, somewhat transparent, wrapped up with a thin membrane. Their vitellus having round shape and yellowish-grey colour, is situated in the centre of the eyed egg. The development of the eyed egg of Ohrid bleak occurs at a relatively high temperature of 18 °C to 22 °C. For this reason their embryonal and pre-larval stage is short, the vitellus being resorbed in 10 days. This way the fish passes on the exogenous nutrition just at the time when the lake including the species provides food for bleak's larvae (Točko 1960).

In the above-mentioned ontogenetic phases the following morpho-ecological peculiarities were significant: a relatively small number of melanofores and xantofores, weakly developed embryonal blood system, insufficiently developed pectoral fins, mouths. A few days after the appearance and differentiation of the maximal number of myomeres, several of them disappeared owing to the differentiation of urostyles in the caudal region being also the case in the embryonal development of the other Teleostei in Lake Ohrid and of other bony fishes, in general (Krizhanovsky 1949, Točko 1959, 1960).

Contrary to the Ohrid bleak being typical phytophilous fish, Prespa bleak and Skadar bleak are litophilous forms. In addition, the spawns of the Prespa and particularly the Skadar form of these species are larger. The diameter of the eyed eggs of Skadar bleak is large compared to other members of this genus (*Alburnus*; 5.5 mm) (Ivanović 1964). It should be taken as a special characteristic of this population if we can accept the above-mentioned data as definite.

Embryonal and larval development of the above-mentioned forms shows similar morpho-ecological properties with the corresponding ontogenetic phases in the development of the other representatives of genus *Alburnus* (Krizhanovsky 1949, Točko 1960).

Passing to exogenous nutrition is followed, at least under artificial conditions, especially in cold water, by a great mortality which can reach over 90 per cent. Larvae grew mostly at their growing edges, and least in the central part of the body; the same is the case with larvae of the other Ohrid and Prespa cyprinids and of cyprinids in some other biotopes in Europe and, in particular, in the Balkans (Stanković 1921, 1925, Točko 1960).

The rate of the average annual growth concerning length, weight and coefficient, too, is most intensive in the first and second years; after that it

TABLE 4

*Average yearly increment in length in cm (1 and 2) and in per cent (3 and 4)*

| Species | Age | | | | |
|---|---|---|---|---|---|
| | $l_1$ | $l_2$ | $l_3$ | $l_4$ | $l_5$ |
| 1. Ohrid bleak | 3.5 | 2.3 | 1.7 | 1.4 | |
| 2. Skadar bleak by B. Ivanović | 4.47 | 3.11 | 2.34 | — | |
| 3. Ohrid bleak | 83.30 | 29.80 | 17.08 | 11.9 | |
| 4. Skadar bleak by B. Ivanović | 66.80 | 27.40 | 16.80 | — | |

considerably decreases. At the same time it is remarkable that the absolute values of length and weight for the Skadar bleak, for one and the same age are considerably greater due to its place in the lake ecosystem (Točko 1969) (Tables 4 and 5).

TABLE 5

*Average yearly increment in weight in g (1 and 2) and in per cent (3 and 4)*

| Species | Age | | | | |
|---|---|---|---|---|---|
| | $1_1$ | $1_2$ | $1_3$ | $1_4$ | $1_5$ |
| 1. Ohrid bleak | 4.1 | 4.7 | 3.5 | 4.2 | |
| 2. Skadar bleak by B. Ivanović | 7.16 | 10.73 | 12.43 | — | |
| 3. Ohrid bleak | 75.00 | 49.40 | 24.60 | 23.10 | |
| 4. Skadar bleak by B. Ivanović | 42.90 | 45.90 | 25.60 | — | |

Analysis of the length classes of Ohrid bleak (Fig. 2) shows that the commonest are length classes from 95 to 105 mm, from 85 to 95 mm, and from 105 to 120 mm. Classes under or over these values are minimal. The diagram illustrates some of the samples from the vegetative and sexual phases. The corresponding differences in weight classes are given; age classes $2^+$ and $3^+$ are mostly present there. Analysis of Prespa and Skadar bleak catch shows close similarity in length, weight and age as well, taking into consideration the corresponding greater dimensions of length and weight from classes of the same age.

The sex relationship of the Ohrid bleak varies, depending on season, age and length classes similar to Prespa bleak and Skadar and to other fishes.

Nutrition of Ohrid bleak has been studied in all its basic ontogenetic phases at the different localities of the lake, and it proved to be planktonic and selective (Točko 1960, 1967). During the larval phase, particularly at its beginning, the nutrition is relatively more diverse as a result of the presence of Rotatoria and planktonic desmids in the intestinal content. But at the end of the larval phase they are rarely found and in the intestinal content the Copepoda and Cladocera, *Diaptomus* and *Daphnia pulex*, and in certain cases, even *Cyclops* species dominate. The representatives of Copepoda dominate in the food of Prespa forms. The Skadar bleak shows the same characteristics concerning food (Ivanović 1964).

It is well known that Lake Ohrid is a salmonid lake (Stanković 1960) unlike Lakes Prespa and Skadar. These two although oligotrophic are cyprinid lakes. In Lake Prespa, Prespa bleak (*Alb. alb. belvica*) and undermouth (*Chondrostoma nasus prespensis*) dominate fish. Lake Skadar is dominated by Skadar bleak (*Alb. alb. alborella*). Although in Lakes Prespa and Skadar trouts are present, the morphometrical factor, i.e. the relatively small volume of the hypolimnion, limits their abundance leading to a very small size, although basically they are real predators and plankton-eaters, and sheat fish, pike and other predators are absent. This is the circumstance that determines the dominating place of the Prespa and Skadar form in

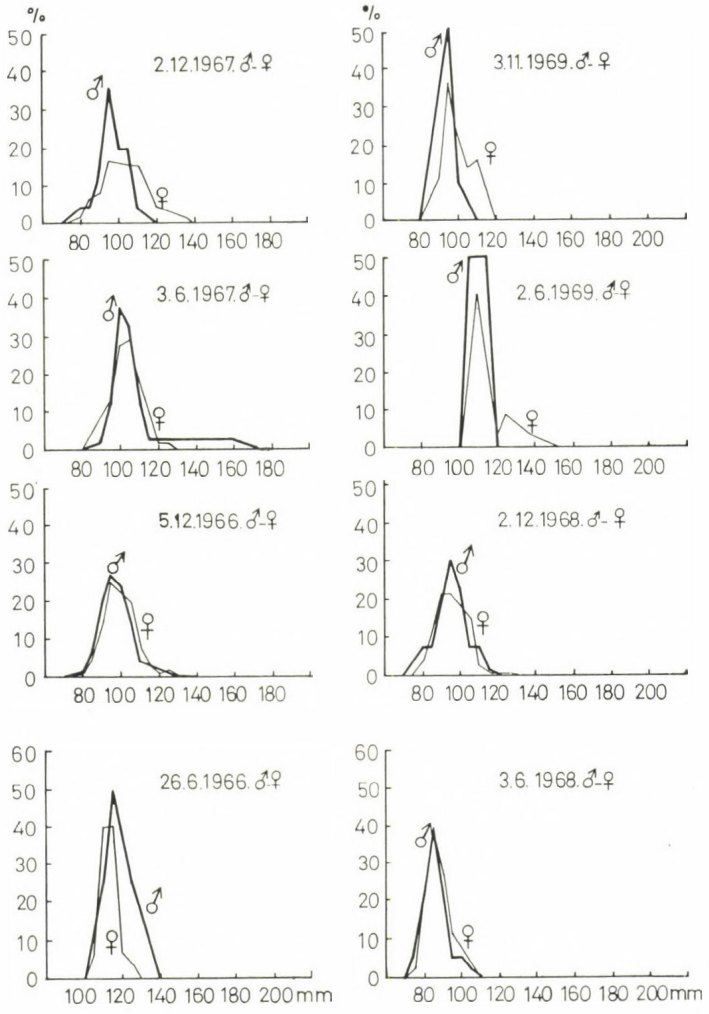


Fig. 2. Length classes of Ohrid bleak in per cent of the total samples (specimens)

these lacustrine ecosystems. In Lake Ohrid, however, thanks to the larger hypolimnion, i.e. homothermal lacustrine zone, and to favourable conditions in the greater part of the upper, heterothermic zone, the larger Ohrid trout, *Salmo letnica* Kar., has become its dominant fish amounting to more than 40 per cent of the total annual fish catch. Trout as characteristic plankton-eater and predator of Ohrid bleak at the same time has become the dominant fish in the lake in the absence of other more characteristic and larger plankton-eaters and predators. In a hard competition with other forms using the same ecological niche, planktonic Copepoda and Cladocera populations of Ohrid bleak have been pushed to the second place and restricted to the littoral region of the lake where the trout stays for a relatively short period

of the year. It is for the same reason that the absolute values of the weight and age classes are smaller. These values are stressed by the relatively lower temperatures of Lake Ohrid in comparison with Lake Skadar, conditionating relatively less intensive metabolism, particularly in the summer period (Točko 1967). In favour of this statement are data about bleak and trout catch in the last decade where the bleak catch is in inverse ratio to the trout catch.

All this, as well as caloric values of Ohrid bleak (Šapkarev 1958) led to the conclusion that it is a significant component of the lacustrine ecosystem.

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